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Survey of Adult Morphology in Nystaleinae and Related Neotropical Subfamilies (Noctuoidea: Notodontidae)

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Abstract. Based on a comparative study of 71 neotropical and 10 palearctic genera, morphological trends in Nystaleinae were ascertained. Over half the nystaleine species were examined (135 of 253). A diverse sample of neotropical Heterocampinae (27 of 37 neotropical genera, 46 species) and Hemiceratini (7 of 11 genera, 15 species) was also surveyed. Additional palearctic and nearctic notodontid species were examined in the more general study.

Survey results are presented along with illustrations of cephalic, thoracic and abdominal structures. Previous interpretations of internal tympanal structures are discussed, and sexually dimorphic structures described and illustrated. A checklist of nystaleine genera is provided. New morphological terms are proposed and synonyms are noted.

INTRODUCTION

The family Notodontidae (Lepidoptera: Noctuoidea) consists of approximately 3,200 species worldwide (Holloway, Bradley, and Carter, 1987). The greatest diversity, over 1300 species, occurs in the New World tropics. Adults are usually heavy-bodied moths with pilose vestiture and cryptic coloration. Wingspans range from 127 mm (*Anurocampa mingens* Herrich-Schäffer, female) to as small as 20 mm (*Talmeca curtoides* Dognin, female). Notodontid larvae are notable for their often bizarre morphology, and some possess unique chemical defenses (cyanic acid, formic acid, and other ketones: Blum, 1981). Many species undergo striking ontogenetic changes between larval stadia, particularly in the Heterocampinae (Packard, 1895; Godfrey and Appleby, 1987). Notodontid larval host plants include both monocots and dicots (the majority on woody dicots), and larvae are usually either monophagous or oligophagous (Miller, 1992).

Little descriptive morphology is available for neotropical Notodontidae. Notodontid morphology is either discussed very generally based on few examples at the family or superfamily level (e.g., Brock, 1971; Richards, 1932), or discussed for only a few species within a faunal treatment or generic revision (e.g., Forbes, 1939a, 1948; Franclemont, 1948; Thiaucourt, 1975, 1980, 1985, 1987). Only recently has a comparative study among subfamily representatives been published (Miller, 1991).

In this paper, I describe and illustrate cephalic, thoracic and abdominal structures found in many notodontids, concentrating on Nystaleinae

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(Tables 1, 2). The checklist of nystaleine genera (Table 1) is assembled from Weller (1989). Many of the following descriptions are new, because previous workers have concentrated on nearctic taxa. Most of my findings concern Nystaleinae, but I also comment on other taxa that illustrate character novelties or important character distributions. Previous interpretations of tympanal structures are discussed, and putative, pheromone-producing structures in males and females are described and illustrated. A summary of morphological terms and proposed equivalents is included.

MATERIALS AND METHODS

Preparation of specimens

Body parts (abdomens, appendages) or entire specimens (except wings) were softened in hot 10% KOH, then cleaned in several rinses of 40% ethanol. Genitalia were stained with either chlorozol black (dissolved in 20% ethanol), or with chlorozol black followed by saffranin (dissolved in 95% ethanol). Stained preparations were positioned, dehydrated, and mounted in either balsam or euparol. The membranous pleats of male genitalia trap water. Best dehydration results were obtained when positioned genitalia were left in sealed dissecting dishes of 95% ethanol for 4-12 hours. Antennae, labial palpi and legs were treated similarly, except that they were not stained. Wings were bleached, stained with Eosin Y, and mounted in balsam.

Softened whole-body preparations were prepared by first removing the abdomen. Either the head and prothorax were removed as a unit, or just the metathorax was removed. Once the viscera and scales were removed, preparations were stained with chlorozol black to enhance membrane contrast with the cuticle.

To examine the recessed tympanal membrane, I rotated the body wall so that the venter was 10 to 30 degrees above horizontal. Different preparations were used to expose the tympanum. In some, the isolated metathorax was entire. In others, midline dorsal and lateral cuts were made. The most satisfactory tympanal preparations resulted when the first abdominal tergum was left connected to the metathorax. In Table 3, the number of preparations is summarized. A complete list of species, sex, dissection numbers and type of dissection (e.g., whole body, genitalia) is available in Weller (1989).

Sources of specimens

Material from the following collections was examined. Abbreviations follow Heppner and Lamas (1982): AMNH, American Museum of Natural History, New York (F.H. Rindge); BMNH, British Museum (Natural History), London (A. Watson); CAS, California Academy of Sciences, San Francisco (P.H. Arnaud); CMNH, Carnegie Museum of Natural History, Pittsburgh (J.E. Rawlins); CNC, Canadian National Collection, Ottawa, Canada (J.D. Lafontaine); CU, Cornell University, Ithaca, New York (J.K. Liebherr); DJ, D. Janzen, private collection, Univ. of Pennsylvania; LACM, Los Angeles County Museum, California (J.P. Donahue); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (J. Carpenter); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (R. Poole, R.K. Robbins); SJW, S.J. Weller preparation, University of Minnesota Insect Collection; UMO,

Table 1. Checklist of nystaleine genera examined (modified from Weller, 1989). Descriptions of new genera, and justifications of other taxonomic changes are given in Weller (1989, in prep.). Type species of new genera are provided below.

NYSTALEINAE: NYSTALEINI

- Ankale Weller, NEW GENUS
  - Lepasta, of authors [not Möschler, 1878]
    - grammodes Felder, 1874 [Nystalea] NEW COMBINATION
      - conspicua Butler, 1878a [Lepasta] NEW SYNONYMY
- Antiopha Schaus, 1901
  - Tachuda Schaus, 1901, NEW SYNONYMY
  - Naduna Schaus, 1901, NEW SYNONYMY
- Bardaxima Walker, 1858b
  - Gisara Schaus, 1901 NEW SYNONYMY
  - Gozarta Walker, 1869
- Calledema Butler, 1875
  - Pseudantiora Kirby, 1892 REVISED STATUS
  - Dasippia Draudt, 1932 NEW SYNONYMY
  - Hippia, of authors [not Möschler, 1878]
- Elasmia Möschler, 1886 REVISED STATUS
  - Edema, of authors [not Walker, 1855]
  - Harma Walker, 1858a NEW SYNONYMY
  - Hippia, of authors [not Möschler, 1878]
- Elymiotis Walker, 1857b
  - Bardaxima, of authors [not Walker, 1858b]
  - Cicynna Walker, 1858a
  - Edema, of authors [not Walker, 1855]
  - Gisara, of authors [not Schaus, 1901]
  - Nystalea, of authors [not Guenée, 1852]
  - Symmerista, of authors [not Hübner, 1821]
- Euxoga Möschler, 1878
  - Ctianopha Schaus 1901, NEW SYNONYMY
  - Lysana, of authors [not Möschler, 1883]
- Gopha Walker, 1862
- Kryptokalos Weller, NEW GENUS
  - Heorta, of authors [not Walker, 1858c]
    - cilla Dognin, 1908 [Hippia] NEW COMBINATION
      - mitis Schaus, 1911 [Heorta]
      - oculata Dognin, 1909 [Lysana]
- Lepasta Möschler, 1878
  - Antiopha, of authors [not Schaus, 1901]
  - Nystalea, of authors [not Guenée, 1852]
- Lyricinus Weller, NEW GENUS
  - Etobesa, of authors [not Walker, 1865b]
  - Proelymiotis, of authors [not Schaus, 1901]
    - xylophasioides Butler, 1878 [Etobesa], NEW COMBINATION

Lysana Möschler, 1883
    Proelymiotis, of authors [not Schaus, 1901]
Marthula Walker, 1856
    Edema, of authors [not Walker, 1855]
    Hippia Möschler, 1878, NEW SYNONYMY
    Phastia, of authors [not Walker, 1862]
    Pseudodryas, of authors [not Möschler, 1878]
    Xanthia, of authors [not Guenée, 1852]
Notoplusia Schaus, 1901
    Chadisra, of authors [not Walker, 1862]
    Crinodes, of authors [not Herrich-Schäffer, 1855]
    Rincodes Schaus, 1901, NEW SYNONYMY
Nystalea Guenée, 1852
    Antiopha, of authors [not Schaus, 1901]
    Congruia Dyar, 1908
    Cyrrhesta Walker, 1857b
    Eunystalea Grote, 1895
    Heterocampa, of authors [not Doubleday, 1841]
    Proelymiotis Schaus, 1901
Phedosia Möschler, 1878
    Bardaxima, of authors [not Walker, 1858b]
Phyllopalpia Draudt, 1932
    Antiopha, of authors [not Schaus, 1901]
Poresta Schaus, 1901, REVISED STATUS
    Edema, of authors [not Walker, 1855]
    Proelymiotis, of authors [not Schaus, 1901]
    Nystalea, of authors [not Guenée, 1852]
    Strophocerus, of authors [not Möschler, 1883]
Strophocerus Möschler, 1883
    Antiopha, of authors [not Schaus, 1901]
    Nystalea, of authors [not Guenée, 1852]
    Poresta, of authors [not Schaus, 1901]

NYSTALEINAE [SENSU LATO]
Bahaia Dyar, 1924
    Betola of authors [not Schaus 1901]
Dasylophia Packard, 1864
    Drymonia, of authors [not Hübner, 1819]
    Edema, of authors [not Walker, 1855]
    Elymiotis, of authors [not Walker, 1857b]
    Heterocampa, of authors [not Doubleday, 1841]
    Oedemasia, of authors [not Packard, 1864]
    Phalaena, of authors [not Linnaeus, 1758]
    Proelymiotis of authors [not Schaus, 1901]
    Symmerista, of authors [not Hübner, 1821]

Didugua Druce, 1891
Euharpyia Schaus, 1901
Lusura Walker, 1855
    Tifama Walker, 1855
    Chaetognatha Felder, 1874
Notela Schaus, 1901
Pentobesa Schaus, 1901
    Edema of authors [not Walker, 1855]
    Betola Schaus, 1901
    Nycterotis, of authors [not Felder, 1874]
    Proelymiotis of authors [not Schaus, 1901]
    Symmerista of authors [not Hübner, 1821]
    Tifama of authors [not Walker, 1855]
Symmerista Hübner, 1821
    Edema Walker, 1855

Table 2. List of other notodontid genera and species examined. Classification follows Forbes (1935), Weller (1989), Miller (1991), and Miller and Otero (1994).

Subfamily: Genus species

DIOPTINAE
Dioptini
    Dioptis trailii Butler
    Phryganidia californica Packard
Josiini
    Erbessa unimacula (Warren)
    Josia sp.
    Scotura nervosa Schaus

DUDUSINAE
    Dudusa sommeri (Hübner)
    Crinodes bellatrix Stoll
    Crinodes sp.

HEMICERATINI[1]
    Antaea juturna Cramer
    Apela strigatula Forbes
    Apela sp.
    Hapigia curvilinea Schaus
    H. nodicornis Guenée
    Hemiceras near *pallidula* Guenée
    Hemiceras sp.

HETEROCAMPINAE
Heterocampini
- *Heterocampa astarte* Doubleday
- *H. astartoides* Benjamin
- *H. guttivitta* (Walker)

Stauropini
- *Stauropus fagi* (Linnaeus)

Tribal affiliation unknown
- *Chadisra bipars* Walker
- *Chadisra* sp.
- *Disphragis notabilis* (Schaus)
- *D. tharis* (Stoll)
- *Farigia* sp.
- *Heorta roseoalba* Walker
- *Litodonta hydromeli* Harvey
- *Malocampa bolivari* (Schaus)
- *Pamcoloma marita* Schaus
- *Rhuda dimidiata* (Herrich-Schäffer)
- *R. focula* (Cramer)
- *R. splendens* (Druce)
- *Rifargia lineata* (Druce)
- *Rifargia* near *mortis* Schaus
- *Rifargia* near *onerosa* Schaus
- *Talmeca perplexa* Schaus
- *Urgedra striata* Druce

NOTODONTINAE
Dicranurini
- *Cerura vinula* (Linnaeus)

Notodontini
- *Pheosia gnoma* (Fabricius]
- *P. tremula* (Clerck)

PHALERINAE
- *Datana ministra* (Drury)
- *Nadata gibbosa* (J.E. Smith)

PYGAERINAE
- *Clostera curtula* (Linnaeus)

THAUMETOPOEINAE
- *Gazalina* sp.
- *Thaumetopoeia processionea* (Linnaeus)

INCERTAE SEDIS

Anurocampa mingens Herrich-Schäffer
Canodia difformis Herrich-Schäffer
Lirimiris lignitecta Walker[1]
Lirimiris sp.[1]
Lobeza Smithi Druce
Zelica myops (Felder)
Zelica zelica (Stoll)
Zelica sp.

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[1] Miller (1991) places Hemiceratini and *Lirimiris* as *incertae sedis*

Table 3. Summary of specimens dissected. Classification follows Miller (1991)(M = male, F = female, g = genitalic preparation, w = whole body preparation).

Taxon	No. of Genera		No. of Species		No. of Preparations			
	Total	Examined	Total	Examined	M-g	F-g	M-w	F-w
Nystaleinae	31(25)[1]	31	253	170	309	147	34	9
Heterocampinae	37	30(3[2])	398[3]	34(4[2])	50	34	12	3
Hemiceratini	11	7	287	9	10	5	4	2
Dioptinae	40	3	400	3	4	5	3	3
Notodontinae	9[3]	1(2[2])	14[3]	2(2[2])	6	6	1	0
Dudusinae	7+[4]	2	93+[4]	3	3	1	1	0
Phalerinae	6+[4]	5	88+[4]	5	6	5	1	1
Pygaerinae	?[4]	1	?[4]	1	6	4	4	0
Lirimiris	1	1	16	2	2	1	0	0
Thaumetopoeinae	23	2	100	3	5	3	1	1

[1] 25 genera after revision (Weller, 1989)
[2] Old World taxa
[3] New World taxa only
[4] Estimates tentative or unavailable (= ?) (Miller 1991)

University Museum, Oxford University, Oxford, England; VOB, V.O. Becker, private collection, Brasilia, Brazil; ZMHB, Zoologisches Museum an der Humboldt-Universität zu Berlin, DDR-Germany (H.J. Hannemann). Figures list the museum collection and source slides or whole body preparation numbers (e.g., AMNH genitalia preparation SJW219).

Terminology

Terminology for genitalic structures follows Forbes (1948), Sibatani et al. (1954), Sibatani (1972), and Klots (1970), except where I propose new terms. Terminology for the tympanum follows Richards (1932), Forbes (1916), and Kiriakoff (1950a), with reinterpretations of some structures. A lexicon and definitions of terms applicable to notodontid morphology is provided.

MORPHOLOGY AND DISCUSSION

Head (Figures 1-3)

The notodontid vertex is usually tightly scaled. Ocelli are present in some species (Forbes, 1948), but can be absent (e.g., *Litodonta hydromeli*: Heterocampinae). Often, a broad band of demelanized cuticle connects the ocelli across the vertex. In most species, the ocelli are located dorsal to the antennal scape and bordering the compound eyes (Fig. 1). The compound eyes are well developed, and the ocular index (frons width/ eye height) (Davis, 1975) ranges from 0.25 (*L. hydromeli*) to 1.0 (*Gazalina* sp.: Thaumetopoeinae) (Table 4). That is, *L. hydromeli* has very large eyes, and *Gazalina* sp. has very small eyes. Presumably, the ocular index and similar measures (eye width/frons width; Ferguson, 1985) reflect degree of night vision acuity. I have not surveyed intraspecific or intrageneric variation. Ferguson (1985) found that eye size may vary seasonally and geographically in arctiids.

The ventral border of the compound eyes and ventrum of the occiput often have long scales and hairs that partially cover the lower eye portion.

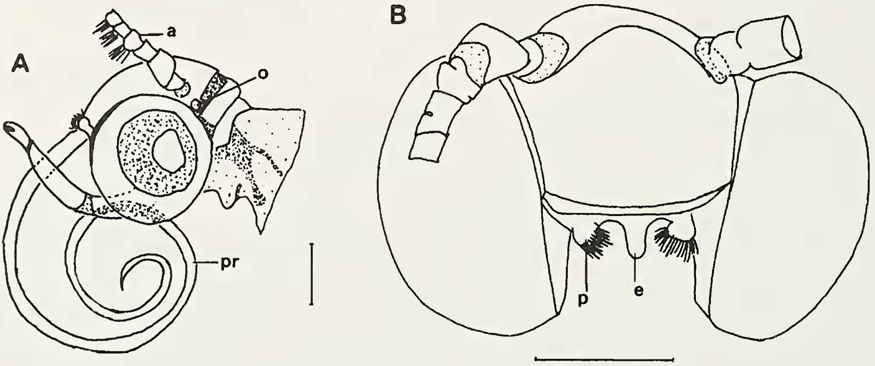

Figure 1. Descaled head of *Rifargia lineata* (NMNH 43,488, male). A. lateral view; B. frontal view. a = antenna, e = epipharynx, o = ocellus, p = pilifer, pr = proboscis. (Scale = 1.0 cm)

Table 4. Mouthpart structure development in the Notodontidae. a = absent, b = bumps, f = female, F/E = frons/eye ratio, ls = lacks setae, m = male, me = membranous, r = reduced, s = short, sc=sclerotized, se = setae present, prep# = dissection number, wd = well-developed, v = vestigial, vs = very short, + = present, - = absent.

Genus species	Prep#	Frons	Eye	Condition of				
				F/E	Pilifer	Proboscis	Maxillary palps	
		width F(mm)	diameter E(mm)				No. of segments	Development
Calledema sp.	f346	1.0	1.92	0.52	+	wd	1	me
Cerura vinula	m340	1.12	2.00	0.56	ls	vs	a	-
Chadisra bipars	m437	0.72	1.72	0.42	+	vs	1	me
Crinodes sp.	m449	1.68	3.24	0.52	+	wd	1	me
Dasylophia anguina	m340	0.80	1.72	0.47	+	s	1	me
Dudusa sommeri	m443	1.36	2.32	0.59	+	wd	2	me
Elasmia pronax	m426	0.86	2.32	0.37	+	wd	2	me
Elymiotis ancora	m347	1.56	2.36	0.66	+	wd	1	me
Farigia sp.	m258	0.68	1.56	0.44	+	v	1	me
Gazalina sp.	f445	1.36	1.36	1.00	b	a	a	-
Gopha mixtipennis	f363	0.72	1.48	0.49	+	wd	1	s
G. mixtipennis	m364	0.92	1.64	0.56	+	wd	1	s
Hapigia nodicornis	m229	1.92	2.92	0.66	+	wd	1	me
Hemiceras sp.	m262	1.36	1.76	0.77	+	wd	1	me,r
Josia sp.	f259	0.78	0.98	0.80	+	wd	1	ss
Litodonta hydromeli	m352	0.44	1.76	0.25	vs	v	1	me,r
Lysana plexa	m364	1.32	2.08	0.63	+	wd	1	s
Nadata gibbosa	m355	0.80	1.80	0.44	+	v	1	me
Notoplusia clara	m349	0.96	1.80	0.53	+	wd	1	me
Nystalea sp.	m263	1.24	2.80	0.57	+	wd	1	me
Pentobesa basitincta	m395	0.92	1.76	0.42	+	s	1	me
Pentobesa xylinoides	m341	1.2	2.12	0.57	+	wd	1	me
Rifargia sp.	m261	1.44	2.20	0.65	+	wd	1	me
Stauropus fagi	m438	1.0	1.68	0.60	s	b	a	-
Zelica zelica	m451	0.72	1.48	0.49	+	wd	1	me
Zelica sp.	m452	1.0	1.52	0.66	+	wd	1	me

Whether the head vestiture is loose and "fuzzy" or tightly scaled varies between genera, but rarely within monophyletic genera.

Notodontid mouthparts can be absent, vestigial or weakly developed (Forbes, 1948; Bourgogne, 1951; Miller, 1991). For many holarctic species, cerurines and thaumetopoeines, vestigial or weak mouthparts are typical. However, the proboscis is well developed in most tropical notodontids including most Nystaleinae. Maxillary palpi are usually present, but in *Gazalina* are absent. They may be one- or two- segmented (Table 4) and either sclerotized or membranous. The pilifer may be vestigial or well developed with stout setae (Fig. 1B). The size of the epipharynx varies, and its shape can be rectangular, bilobed, or round. When the proboscis is vestigial, associated structures are usually vestigial. Functional mouthparts indicate that adults probably feed and live a long time.

Labial palpi are usually three-segmented, and normally, the length of the third segment is approximately two-thirds the length of the second. However, the third segment can be much longer or much shorter (Fig. 2A-D), or the labial palpus can be reduced to two segments (Miller, 1991). As in most Lepidoptera, the organ of vom Rath is well developed. Typically, labial palpi are tightly scaled, although loose, long hairs can emanate from the first segment.

Notodontid antennae tend to be sexually dimorphic, with males possessing more complicated antennal structures (e.g., pectinations, cilia) than females (e.g., shorter cilia, scattered setae). Occasionally, antennae are monomorphic (*Gopha mixtipennis* Walker). Individual antennal segments can be cylindrical, bulbous or prismatic and an antenna may be composed of a combination of segment types. Segment shape and structure can vary between and within genera. Some examples of antennal variation are shown in Figure 3.

The antennal scape of most notodontids is rounded, although it can be elongate. In some species, compact clusters of scales arise from the scape. Forbes (1948) referred to these as antennal tufts. Antennal tufts may be either short and blunt-tipped (*Lirimiris* Walker), triangular (*Hemiceras* Guenée), or long, (e.g., *Nystalea, Phedosia, Pentobesa, Dasylophia*).

In males of *Hapigia* Guenée, the antennal scape and first segment are greatly modified. The first segment is greatly expanded and bowl-shaped. The pedicel is membranous dorsally and forms a hinge between the scape and first segment. The first segment locks into a groove on the scape, folding the distal part of the antenna over the back (Fig. 3F).

Thorax (Figures 4-6)

The thorax is usually covered dorsally with moderately long scales and ventrally with long scales and hairs. The most obvious modifications occur on the prothorax and metathorax. Mesothoracic sclerites did not appear to vary among taxa.

Prothorax. The patagia are usually sclerotized and covered with scales. They are thought to be homologous with the membranous warts of Trichoptera (caddisflies) (Kristensen, 1984). Caudad to these, a second set of membranous or weakly sclerotized structures occurs in most species (Fig. 4a). These appear to be homologous with the noctuid parapatagia (Oseto and Helms, 1976). Development of parapatagia varies, and they are easily damaged when preparing a whole-body dissection. They are present in both sexes. Occasionally, a second, weakly developed, lateral pair of parapatagia occurs next to the spiracle (not illustrated, e.g. *Gazalina*). *Dudusa sommeri* (Dudusinae) appears to

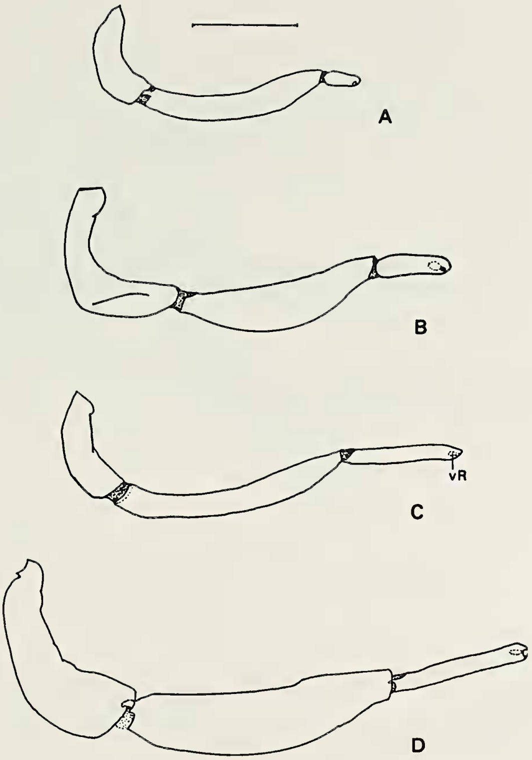

Figure 2 Labial palpi (distal at right). A. *Notoplusia minuta*; B. *Nystalea virgula*; C. *Calledema jocasta*; D. *Nystalea corrusca*. vR = vom Rath's organ. (Scale = 1.0 mm)

possess a derived condition where parapatagia are absent and the patagia are enlarged and heavily sclerotized.

Mesothorax and metathorax. No variation was observed in most sclerites comprising these segments. The metathoracic furcae show some variation, and tympanal studies indicate that some thoracic novelties (e.g., double pocket IV, *Hemiceras* sp.) may be species-specific.

Tympanum and associated structures (Figs. 5, 6). As in other noctuoids, the notodontid tympanum occurs on the metepimeron. Notodontids are unique in that the tympanum is recessed; the tympanal membrane faces ventrally (Forbes, 1916; Richards, 1932; Sick, 1940; Kiriakoff, 1950a, 1950b, 1950c; Miller, 1991). The notodontid tympanal membrane lacks the nodular sclerite (Richards, 1932), and sclerotized abdominal hood associated with tympana in many Noctuidae, Arctiidae and Lymantriidae. In nearly all neotropical and some nearctic notodontids, the first abdominal spiracle occurs in a sclerotized, bowl-like depression which may act as a sound collector. In many holarctic species, the bowl is either weakly sclerotized or membranous. The genera *Hapigia* and

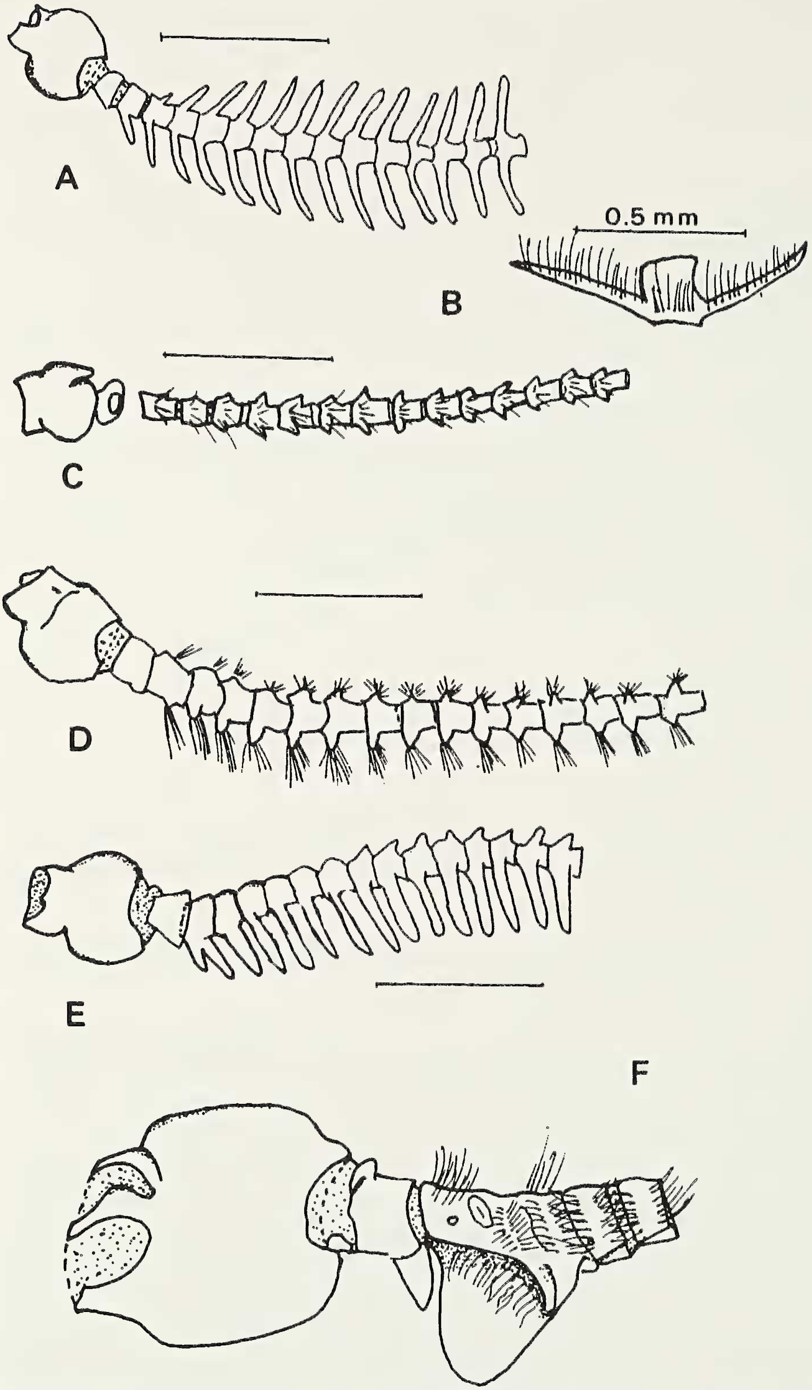

Figure 3 Antennal variation. A. *Notoplusia clara*, male, (bipectinnate); B. enlarged segment showing pectinations and cilia; C. *Notoplusia clara*, female (scattered setae); D. *Elymiotis ancora*, male (ciliate); E. *Canodia difformis*, male (unequally pectinnate); F. *Hapigia nodicornis*, male, showing basal enlargement. (Scale = 1.0 mm)

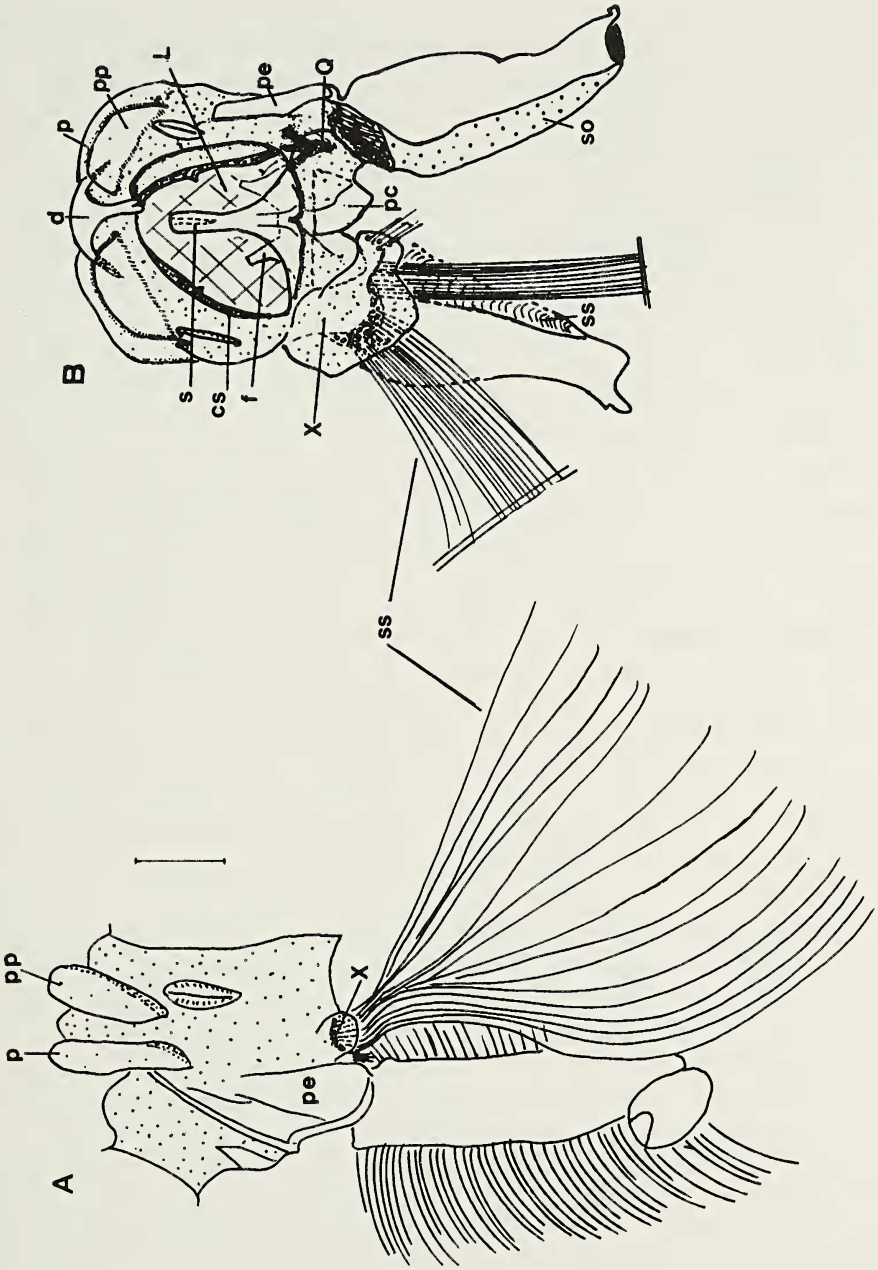

Figure 4 Prothorax of *Hapigia curvilinea*. A. side view, anterior at left; B. posterior view with right scent brush flap removed. cs = cervical sclerite, d = dorsal plate of pronotum, f = furca, L = lumen, p = patagium, pc = precoxale, pp = parapatagium, pe= proepimeron, s = spina, Q = reinforced fusion point of furca, cervical sclerite, and proepimeron, X= modified membranous flap, so = putative scent organ, ss = scent scales. (Scale = 1.0 mm)

Antaea possess a large, membranous, pleural hood inflated with hemolymph that surrounds this sclerotized bowl. With isolated ear preparations, Fullard (1984) demonstrated that the pleural hood helps to localize sound waves, and that it increases the moth's ability to detect the direction of incoming signals.

The internal morphology of the notodontid tympanum has been described by Richards (1932) and Kiriakoff (1950a,b), but their interpretations conflict. Richards (1932) described tympana for the major noctuoid families, concentrating on Noctuidae. His terminology is generally applicable to notodontids.

For notodontids, Richards concluded that pockets I and II were small, pocket III was absent and pocket IV was present. He examined three nearctic species (*Datana angusi* Grote & Robbinson: Phalerinae, *Heterocampa guttivitta* Walker: Heterocampinae, *Clostera inclusa* Hübner: Pygaerinae) and two neotropical species (*Zelica zelica*: Pygaerinae, *Malocampa* near *sorex*: Heterocampinae). Re-examination of *H. guttivitta* shows that Richards misinterpreted the notodontid pockets. From his diagram (plate 10: Richards, 1932), it is apparent that he did not rotate the thorax sufficiently to view the pockets. Internally, notodontid tympana are very different from those of noctuids. The recessed tympanal membrane obscures the pockets, and pocket orientation is skewed. Using position and orientation of pocket openings as criteria of homology, I conclude that pockets I, III and IV are present in most notodontids, and that pocket II is often absent. Pocket II is sometimes difficult to see even when it is present. The notodontid structure that I interpret as pocket III, and that Richards termed pocket II, is positioned at the ventral rim of the tympanic membrane, with its opening into the body cavity facing dorsally (e.g., Fig. 5A).

Kiriakoff used tympanal studies to classify Notodontidae (e.g., Kiriakoff, 1950a, 1950b, 1950c), stressing different shapes of scutal phragma ("type notodontoid" vs. "type phalenoide") and tympanal structures, but Kiriakoff's tympanal interpretations were sometimes inconsistent. Distortion caused by preparing and viewing the thorax may explain discrepancies. For example, Kiriakoff described *Bardaxima marcida* Felder and *Gisara procne* Schaus as having differently shaped tympanal cavities (Kiriakoff, 1950c). *Gisara* is a junior synonym of *Bardaxima* (Weller 1989; Table 1), and the tympanal cavities of these two species are practically identical. Kiriakoff also disagreed with Richard's interpretation of tympanal structures and renamed pocket IV: "le support posterieur" (Kiriakoff, 1950a, 1950c). Notodontid pocket IV is usually open with its edges defined by an anterior and posterior internal ridge that extend from the tympanal cavity (timbal sensu Kiriakoff) to the furcal suture (Fig. 5: IVa, IVp). The anterior ridge (IVa) can be reduced or absent as in several notodontids that Kiriakoff examined (Kiriakoff 1950a, 1950c). In *Crinodes* Herrich-Schäffer, pocket IV is closed (Fig. 5E) like those of

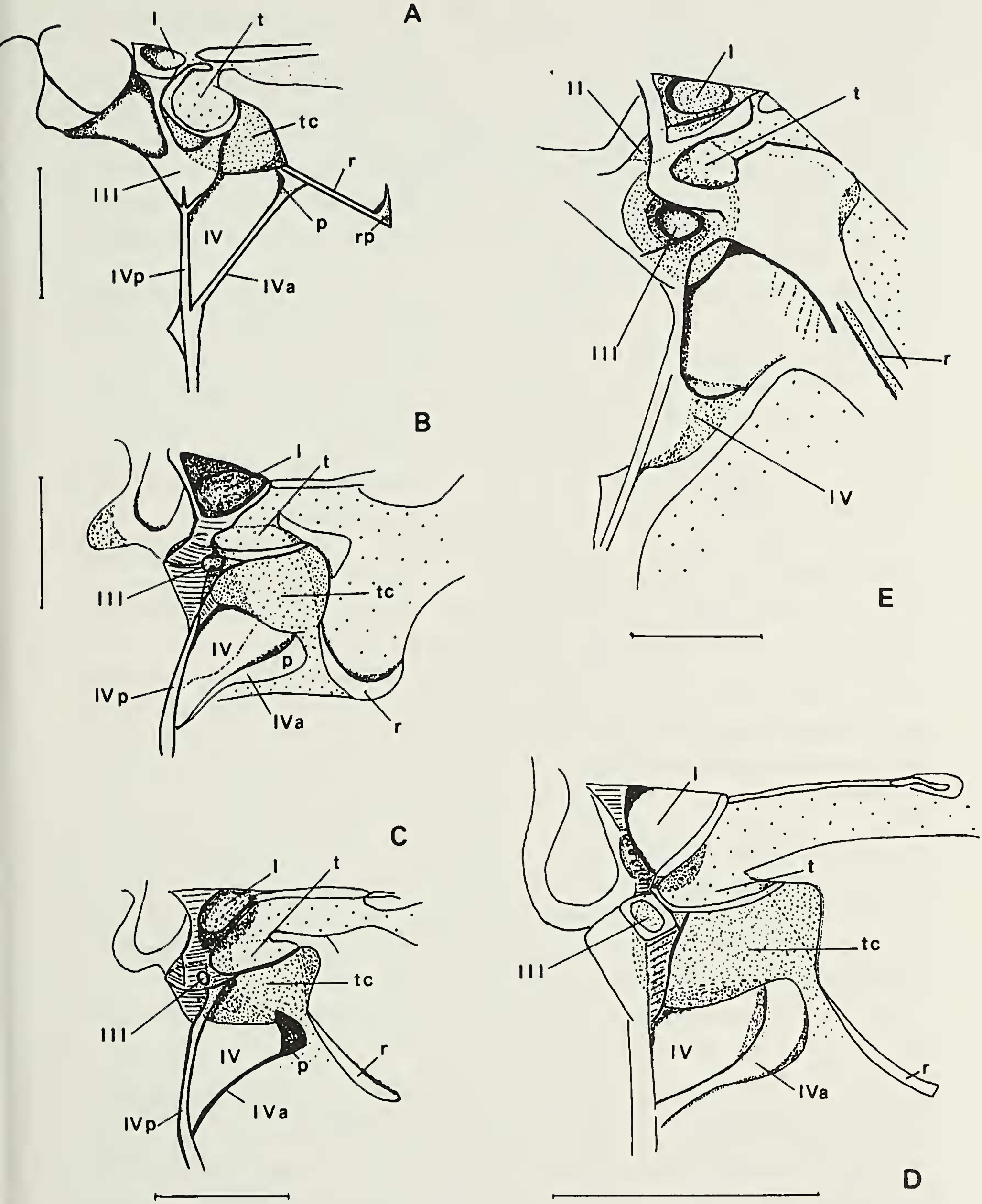

Figure 5 Internal view of notodontid metathoracic tympana, anterior at right. A. *Rifargia lineata*; B. *Elymiotis ancora*; C. *Antiopha multilinea*; D. *Elasmia astuta*; E. *Crinodes* sp. I = pocket I, II = pocket II, III = pocket III, IV = closed pocket IV, IVa = anterior strut of open pocket IV, IVp = posterior strut of open pocket IV, p = anterior branch pocket of IV, r = pre-epimeral/epimeral ridge, rp = ridge pocket, t = tympanal membrane, tc = tympanal cavity. (Scale = 1.0 mm)

Noctuidae, supporting the homology of the posterior ridge of pocket IV and Kiriakoff's "support posterior."

A feature of pocket IV not mentioned by Kiriakoff is the tendency for a small pocket (p) to form on the dorsal end of the anterior support abutting the tympanal cavity (Fig. 5). This additional pocket can be elaborate as in some *Hemiceras*. Also, the degree of divergence between the anterior and posterior supports of pocket IV differs among species. They are normally at acute angles, but can also be at right angles to one another (e.g. *Pentobesa basitincta* Dognin).

In addition to pocket IV, the pre-epimeron/ epimeron boundary is often modified in notodontids. There may be a simple internal ridge or a pocketlike structure (Fig. 5A-E) that originates at the tympanal cavity and extends anteriorly. Kiriakoff termed this structure "support anterior de la timbale" (Fig. 5, r). This support occasionally fuses with the anterior edge of pocket IV as in *Anurocampa mingens* (Kiriakoff, 1950c: his fig. 11). This epimeral pocket and dorsal pocket of the anterior branch of pocket IV may provide additional resonating chambers.

Extensive tympanal variation occurs in the dioptines and thaumetopoeines (Richards, 1932; Sick, 1940). Many dioptines are brightly colored, mimetic and probably diurnal (Hering, 1925; Miller and Otero, 1994). The tympanum may be well developed, or reduced and rudimentary. In the five dioptine species examined, pocket II is absent in all, pocket III is absent in most, and pockets I and IV are absent when the tympanal cavity is rudimentary. In *Scotura nervosa*, *Josia* sp., and *Erbessa unimacula*, pockets I and IV are present and well developed, but pockets II and III are absent (Fig. 6A-C). These species also have a well-developed tympanal concavity that Richards referred to as a kettledrum structure (Richards, 1932: 38). This tympanal type is restricted to a subset of dioptine genera (Sick, 1940; Kiriakoff, 1950a; Miller and Otero, 1994). Miller and Otero (1994) use the presence of this kettledrum tymanal cavity to recognize the Josiini, formerly the Josiinae of Kiriakoff (1950a) and group V of Sick (1940).

The remaining dioptine genera are placed in the Dioptini (Miller and Otero, 1994), because they lack the kettle-drum type cavity. Reduced tympana in dioptines can occur in various ways. In *Dioptis trailii*, all pockets are absent, and the tympanal cavity is represented by a membranous bulge supported by a weakly sclerotized frame. In *Phyrganidia californica*, pocket I is modified and resembles a horizontal, lateral bridge (Fig. 6D). There is a hint of pocket III, and pocket IV is reduced. The tympanal cavity is extremely shallow, and the tympanal membrane is large (Fig. 6D). An external view of this tympanum is illustrated in Miller (1987). Illustrations of internal views of reduced dioptine tympana can be found in Richards (1932), Sick (1940), and Kiriakoff (1950a). I interpret the missing pockets as secondary reductions rather than as primitive absence because Dioptinae are a derived element within Notodontidae (Minet, 1983; Weller, 1989; Miller, 1991).

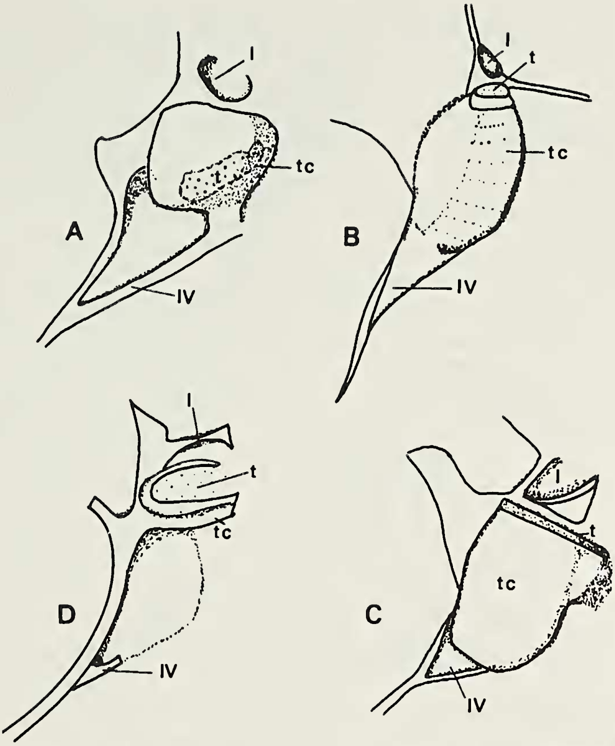

Figure 6 Internal view of dioptine metathoracic tympana. A. *Scotura nervosa*; B. *Erbessa unimacula*; C. *Josia* sp; D. *Phryganidia californica*. I = pocket I, IV = open IV, r = pre-epimeral/epimeral ridge, t = tympanal membrane, tc = tympanal cavity.

I also examined one thaumetopoeine, *Thaumetopoea processionea*. It possesses a large, bowl-like tympanal cavity. Pocket I is represented by a slender bridge, pockets II and III are absent, and pocket IV is reduced (not figured). Whether pocket number and size represent secondary reduction or primitive absence is not known.

Legs (Figures 7-8)

Prothoracic Leg. Modifications of the notodontid prothoracic leg are often sexually dimorphic, with androconial hairs (Table 5). In many Nystaleinae, males possess a prothoracic femur and tibia with modifications typical of pheromone production and dispersal (Figs. 7, 8). The lateral inner surface of the femur has one (e.g., *Bardaxima, Calledema*; Figs. 7B, 8A) or two (e.g., *Nystalea*; Fig. 8B) elliptical, slightly concave areas of membranous cuticle covered with woolly hairs and surrounded by flat, truncate scales with wide lamellae characteristic of androconia (McColl, 1969). Longer hairs overlay these shallow, glandular pockets. Near the proximal articulation of the tibia, a cluster or "pencil" of long scales occurs on a raised patch of cuticle. This pencil lays in a flattened

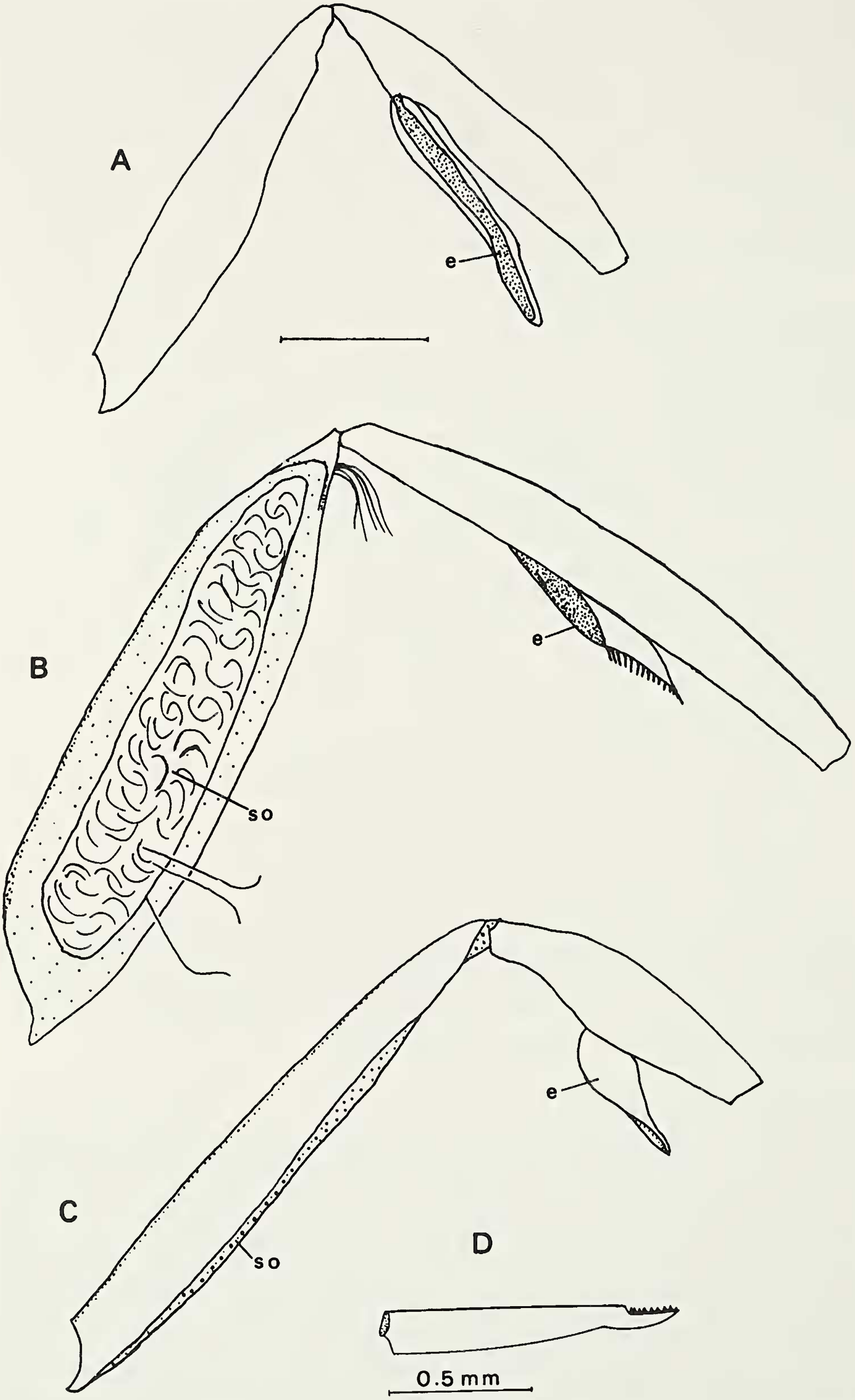

Figure 7 Modifications of male legs. A-C. Prothoracic femur and tibia; A. *Urgedra striata* (normal condition); B. *Bardaxima* sp. (single pocket condition); C. *Apela* sp. (ventral femoral pocket condition); D. *Strophocerus cossoides*, male metathoracic tibial spur serrations. s.o. = putative scent organ, e = epiphysis. (Scale = 1.0 mm)

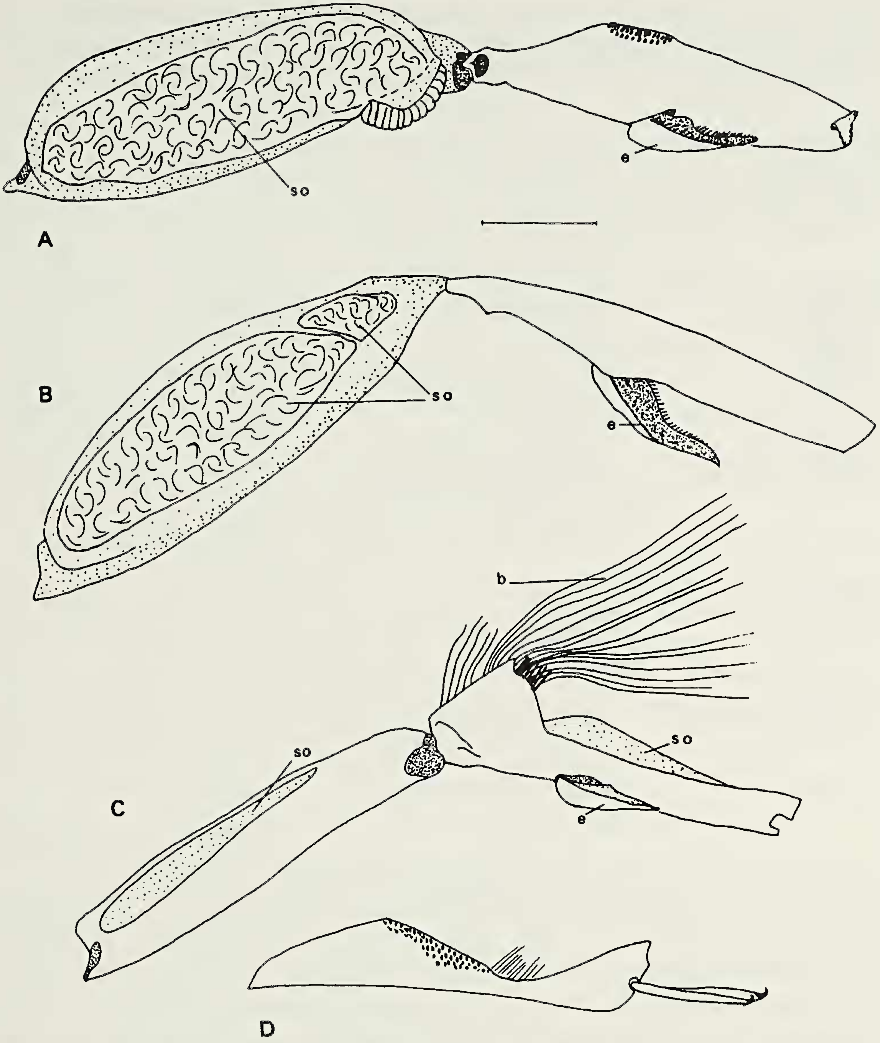

Figure 8 Other leg modifications of males. A-C. Prothoracic femur and tibia; A. *Calledema* sp. (single pocket); B. *Nystalea aequipars* (double pocket). C. *Lysana plexa*; D. *Lysana plexa* (mesothoracic tibia). s.o. = putative scent organ, e = epiphysis, b = distributing pencil. (Scale = 1.0 mm)

area or groove on the ventral, tibial surface, and extend to the first tarsal segment in some species. In *Lysana plexa* Möschler, the surface underlying the tibial hair pencil is also membranous, and the pencil is very large (Fig. 8C).

These femoral organs are analogous to the mesothoracic leg scent organ in some male noctuids (Birch and Hefetz, 1987), and probably have a similar function. Presumably, membranous areas produce short-range pheromones that are distributed by the tibial scent pencil during courtship.

Other modifications of male prothoracic legs can occur. In some species (e.g., *Apela* sp.: Hemiceratini, Fig. 7C), the femur's ventral edge is

Table 5. Male structures with putative courtship function in neotropical Notodontidae (Pt. = prothoracic, Ms = mesothoracic, Mt = metathoracic, s.s. = scent scales, s.h.= hair-like scent scales, s.p.= scent pencil, SSO = saccular scent organ)

Location	Description	Examples
Pt femur	one glandular area	Bardaxima
	two glandular areas	Nystalea
Pt tibia	s.h., s.s. or s.p.	Nystalea, Bardaxima
Ms femur	s.h.,s.s.	Nystalea
Mt tibia	s.h., s.s.	*Hapigia curvilinea*
Mt tibia	tibial spur gibbose	*Calledema marmorea*
Hindwing	stigma	many *Hemiceras*
Pleuron 3 and 4	glandular area, s.h.	*Phedosia turbida*
Sternum 4	cteniophore	many Heterocampinae, *Hapigia*
Sternum 5	peniculus	*Calledema marmorea*
Sternum 8	cuticular brush	*Marthula pulchra*
	posterior edge	*Lyricinus*
Tergum 8	s.h., s.s.	some *Dasylophia*
Sacculus	SSO: pleated, glandular, s.h., s.s.	many notodontids
Sacculus	Barth valve: sacculus enfolds s.p.	most *Hemiceras* *Hapigia*

grooved and surrounded by scent hairs and scales. In *Hapigia* (Hemiceratini), the mesal surfaces of the femur have a single row of stout setae covered with scales (not shown), and long scent scales emanate from the proximal mesal and posterior edges of the coxae (Fig. 4a). Two scent pencils are associated with an enlarged, pleural membrane that enfolds their base (Fig. 4b: X). The furca, cervical sclerite and a ridge emanating from the proepimeron fuse above the coxa, and provide a reinforced, muscle attachment point (Fig. 4b: Q). The insertion points of the pencils are sclerotized. The scent pencil scales extend along the inner surface of the femur, and fan out when the legs are separated. A portion of the mesal coxal surface is modified into membranous cuticle covered with flat androconia (Fig. 4b: so, ss).

The notodontid epiphysis is usually one-third to one-fourth the length of the tibia, and has a comb of stiff setae (e.g., Nystaleinae, Hemiceratini, some Dioptinae and Heterocampinae), although it may be long and flattened with a rough surface (e.g., some *Dasylophia*, some heterocampines, Dicranurini and Thaumetopoeinae) (compare Figs. 7A-C; also Marumo, 1920). The tarsi are spinulose, and as in many Lepidoptera, there are usually two long tarsal setae on the distal end of the fifth tarsomere (Oseto and Helms, 1976). Multiple (usually 4 to 6), long tarsal setae occur in several nystaleine genera (e.g., *Nystalea*, *Elymiotis* Walker, and *Bardaxima*), and number of setae can vary between sexes. Multiple, short tarsal setae occur in *Thaumetopoea processionea*. Tarsal claws on all legs may be single or bifid (= dentelées: Kiriakoff, 1950a; Weller, 1987, 1989, 1990; Miller, 1991), and their apices smooth or serrate (Janse, 1920; Arru, 1965; Weller, 1987, 1989, 1990, Miller, 1991).

Mesothoracic Leg. Usually the femur and tibia are unmodified, and the tibia and tarsomeres are spinulose. Mesothoracic tibiae have one pair of tibial spurs which often have serrations or comblike ridges on their apices (Janse, 1920; Miller, 1991; Fig. 7D). Such tibial spur serrations occur in many notodontids, but they are visible only under high magnifications. They occur in the Dioptinae, but not in *Gazalina* (Thaumetopoeinae). The same condition is found in *Lymantria* Hübner and *Dasychira* Hübner (Lymantriidae) (Miller, 1991).

Metathoracic Leg. In males, the femur and tibia have long hairs and scales arising from the caudal surface. These may disperse pheromones produced from structures on the abdomen (Jordan, 1923) or genitalia (below). There are usually two pairs of tibial spurs, again with tibial spur serrations, but one pair is lost in four unrelated lineages: Thaumetopoeinae, Dicranurini, some Dudusinae and some Heterocampinae (i.e., *Stauropus* Germar) (Miller, 1991). Again, tibia and tarsomeres are spinulose and tibial spurs often serrate.

Wings (Figs. 9, 10)

Wing coloration in Notodontidae tends to be cryptic with subtle patterns (Draudt, 1932). Ground colors of brown or drab green are common, although Dicranurini wings are usually white with black markings. In fresh specimens of *Dasylophia* sp., the brown and black pattern is overlaid with light greens and pinks that give the forewing a lichen and moss covered appearance. These pigments are unstable and fade by the third year after a specimen has been collected. Wing coloration in Dioptinae ranges from gray (*Scotura* Walker) or brown (*Phryganidia* Packard) to bright, mimetic species (e.g., *Josia* Hübner) (Hering, 1925; Miller and Otero, 1994).

In females, number of frenular bristles tends to be constant within monophyletic lineages. The number of bristles is two in Nystaleinae (except *Lusura* with three), and three in Hemiceratini (except *Apela* with two) and Dioptinae surveyed. Number of bristles range from four to six in some Heterocampinae, to many (up to 20) in some Heterocampinae and Thaumetopoeinae (Arru, 1965; Miller, 1991).

Forewing venation sometimes varies within monophyletic genera (e.g., *Nystalea*), and this has led to splitting by workers who relied solely on wing venation to characterize genera. The forewing areole may be present or absent, and the position of veins R2, R5 and M1 can vary

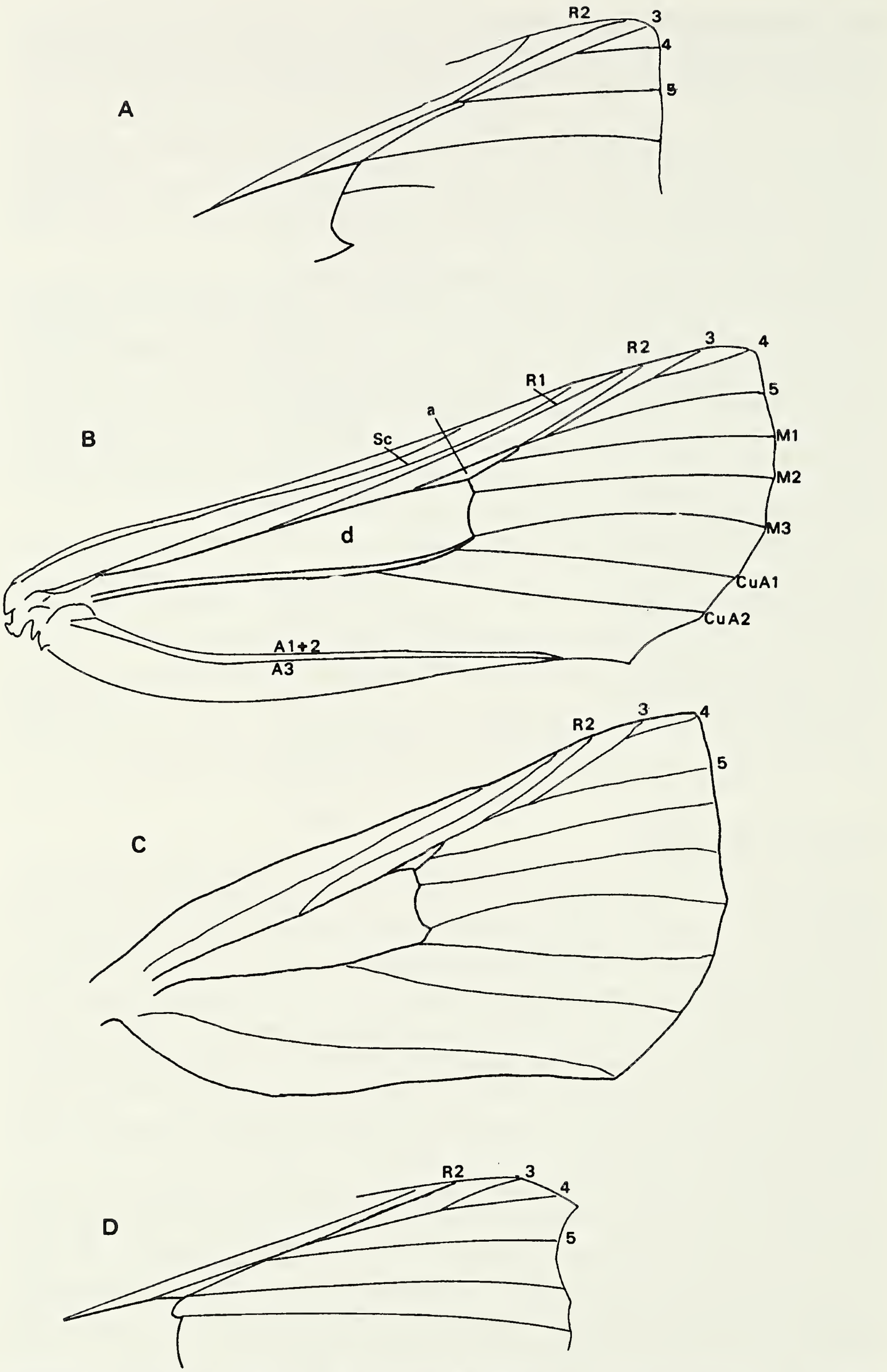

Figure 9 Forewing veins. A. *Bardaxima lucilinea*; B. *Lysana plexa*; C. *Lyricinus xylophasioides*; D. *Calledema rufescens*. a = accessory cell, d = discal cell, Sc = subcostal vein, M1-M3 = medial veins, R1-R5 = radial veins, CuA1-CuA2 = cubital veins, A = anal veins.

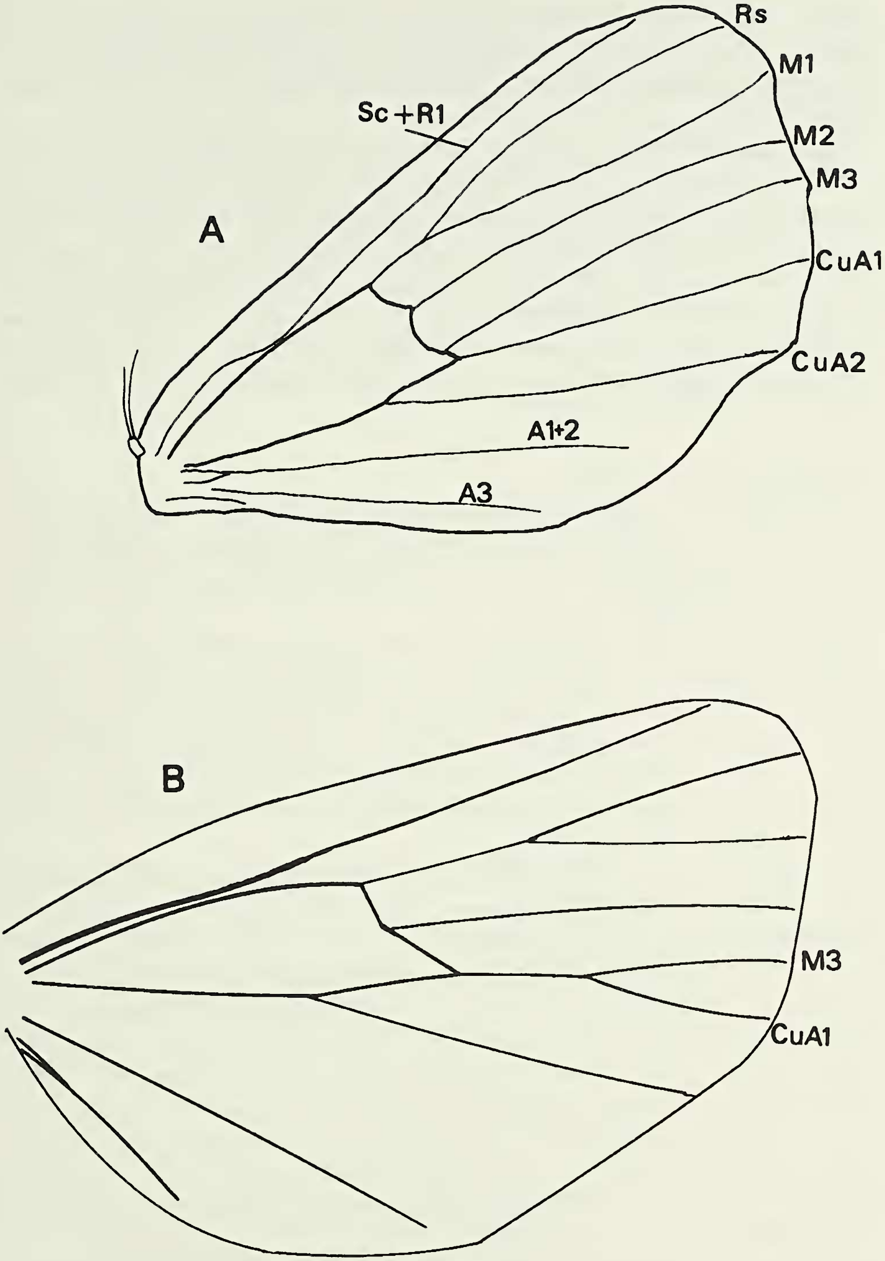

Figure 10 Hindwing veins. A. *Marthula pulchra*; B. *Scotura nervosa*. d = discal cell, Sc+R1 = subcostal and R1 vein, M1-M3 = medial veins, RS = radial sector, CuA1-CuA2 = cubital veins, A = anal veins.

within genera (Fig. 9; Weller, 1989). Vein M2 usually arises from the midpoint of the discal cell or slightly above. In Dioptinae, M3 and CuA1 are usually stalked (Miller, 1987), a condition not found in other notodontids.

Hindwing venation in notodontids is less variable than forewing venation (Fig. 10). Veins Sc-Rs can be connate, short-stalked or long-stalked. Vein M2 arises from the middle of the discal cell except in *Hemiceras* and allies where the vein appears to have been lost. Veins M3 and CuA1 can be separate, connate or stalked. Again, multiple conditions can occur within monophyletic genera. In *Hemiceras* males, approximately two-thirds of the species (total = 150) have a small patch of specialized scales located on or near vein M3, termed a stigma by earlier authors (e.g., Schaus, 1901).

Abdomen (Figs. 11-13)

Modifications of the male second abdominal sternum can occur, and both males and females may have structures for pheromone production and dispersal. Modification of the first abdominal segment is discussed under "Tympanum."

Male. The second abdominal (A2) sternum is usually simple with a faintly de-melanized, semicircular area anteriorly, here referred to as a "window" (Fig. 11A-D). The caudal border of the window is a flexion point. In some genera, these areas are translucent and elaborate (e.g., *Marthula*, *Elasmia astuta* [Schaus]) (Fig. 11C,D,F), and the cephalic edge is often reinforced. In *Antiopha*, this reinforcement is elaborated into a second set of apodemes (Fig. 11B, E).

The pleural region of A2 and A3 may be expanded with membranous or sclerotized outgrowths bearing hair-like scales (e.g., *Crinodes*: Dudusinae, *Phedosia*: Nystaleinae) (Fig. 12C). The cteniophore (Jordan, 1923) occurs on A4. It is a large flap with stout spines and internal levers for muscle attachment (Fig. 12A). The cteniophore is reduced in some species (e.g., *Heterocampa guttivitta*: Heterocampinae) and absent in most. On A5 of some *Calledema* sp. (Fig. 12B), a similar structure occurs. Thiaucourt (1985) named this structure the peniculus (latin: little tail, tuft) — not to be confused with "penicullus," a structure on the tegumen of noctuid male genitalia (Forbes, 1954). The peniculus, cteniophore and other modifications of abdominal pleura II and III appear to be serial homologues.

Tergum 8 may be modified externally with androconia (*Dasylophia* sp.; Fig. 13D), or modified internally for muscle attachments (Fig. 13A-C). Normally, its antecosta is present and well developed. Forbes (1916) showed that in the noctuid *Apamea amputatrix* (Fitch), genitalic retractor muscles (T1 and T2) extend from the eighth antecosta to the tegumen and vinculum. These retractor muscles are widespread in the Lepidoptera (e.g., Forbes, 1939b; Stekolnikov, 1967; Stekolnikov and Kuznetsov, 1986; Tikhomirov, 1979). In Nystaleinae and several addi-

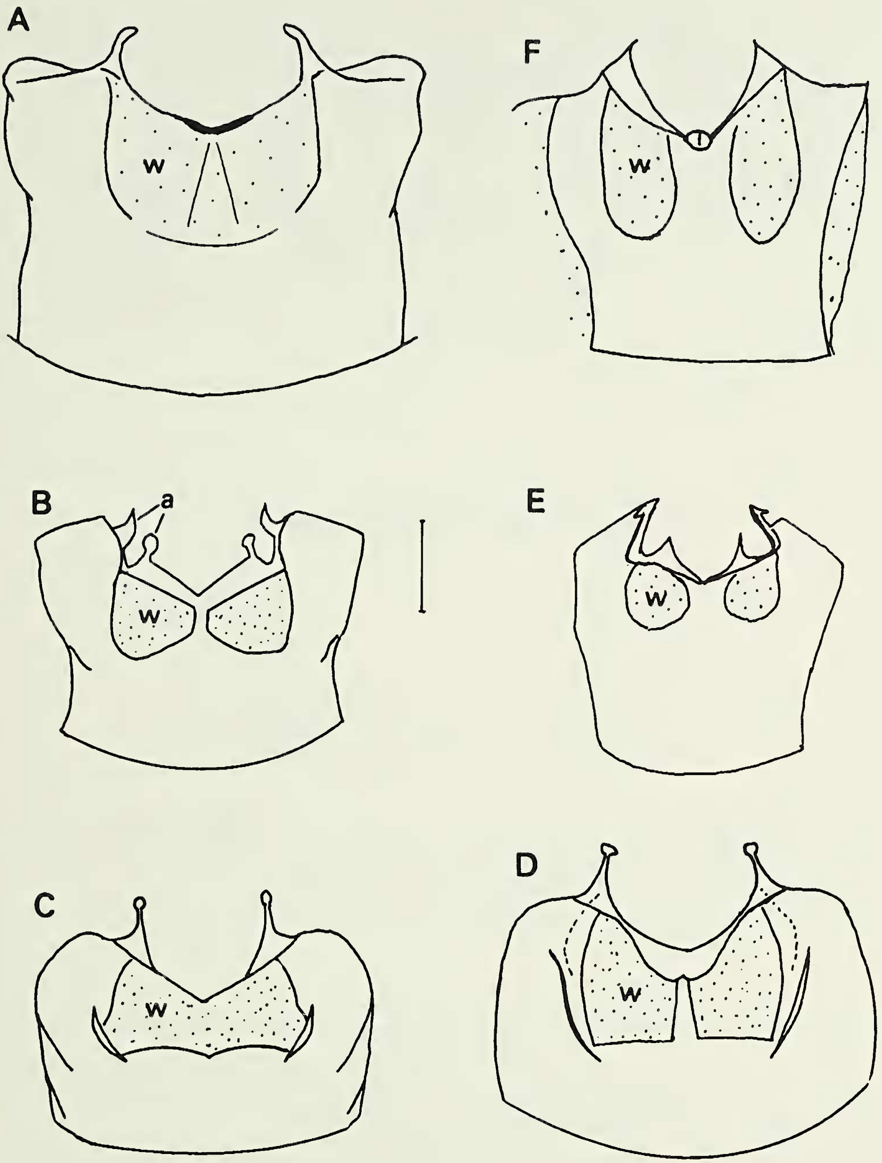

Figure 11 Male second abdominal sternum. A. *Elasmia astuta*; B. *Antiopha discreta*; C. *Marthula pleione*; D. *Marthula griscesens*; E. *Antiopha multilinea*; F. *Kryptokalos cilla*. a = antecostal apodeme, w = window. (Scale = 1.0 mm)

tional neotropical genera, the antecosta is weak or absent. Tergum 8 is usually medially divided with either a mid-dorsal plate or paired ridges for muscle attachment (Fig. 13A-D). Presumably, the T1 and T2 muscles have shifted their insertion from the cephalic edge to the mid-dorsal region of the tergum in these species. This shift appears to be correlated

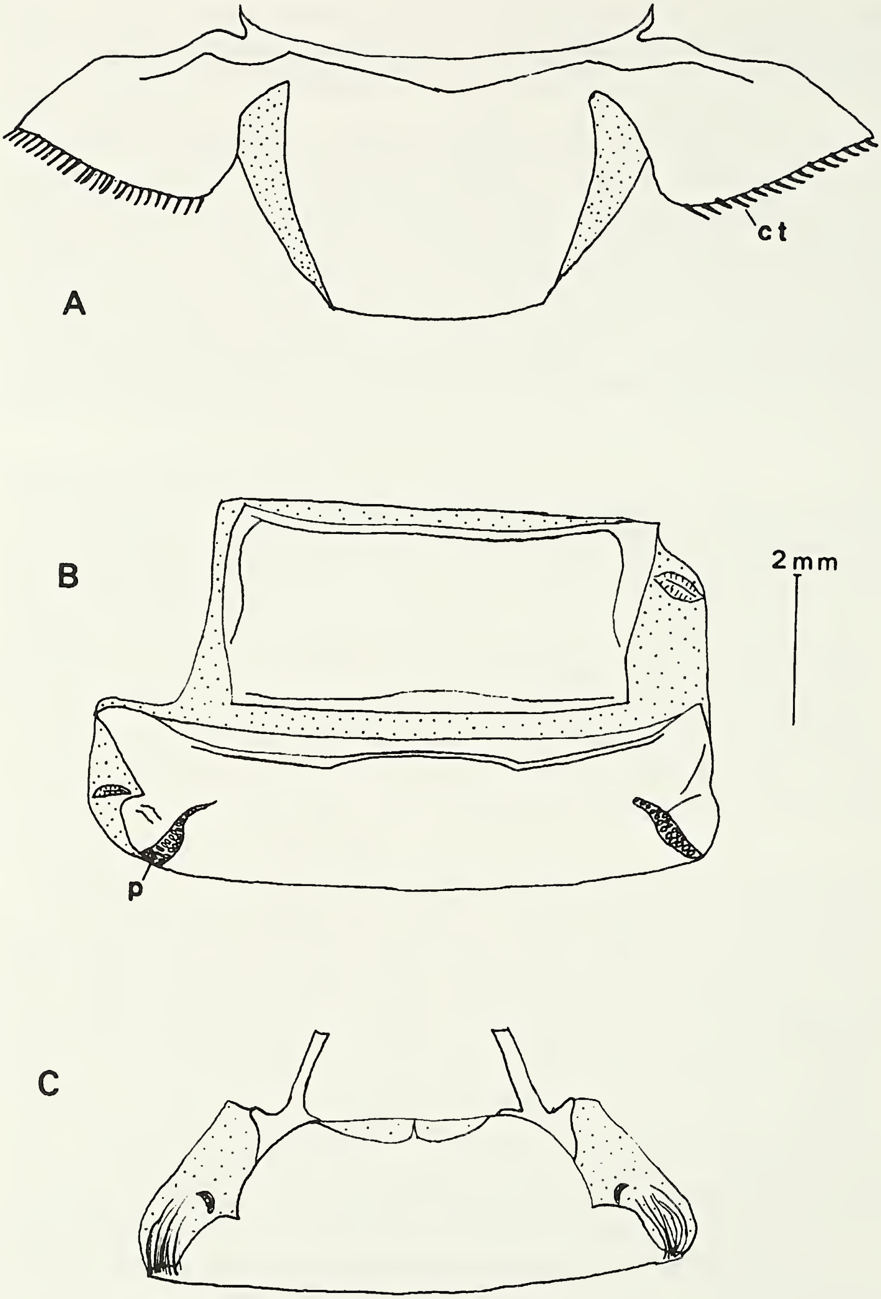

Figure 12 Male abdominal structures with probable courtship function. A. Sternum 4, cteniophore (*Hapigia* sp.); B. Sterna 4 and 5, peniculus (*Calledema jocaste*); C. Tergum 2 (*Lysana plexa*). ct = cteniophore, p = peniculus. (Scale = 2.0 mm)

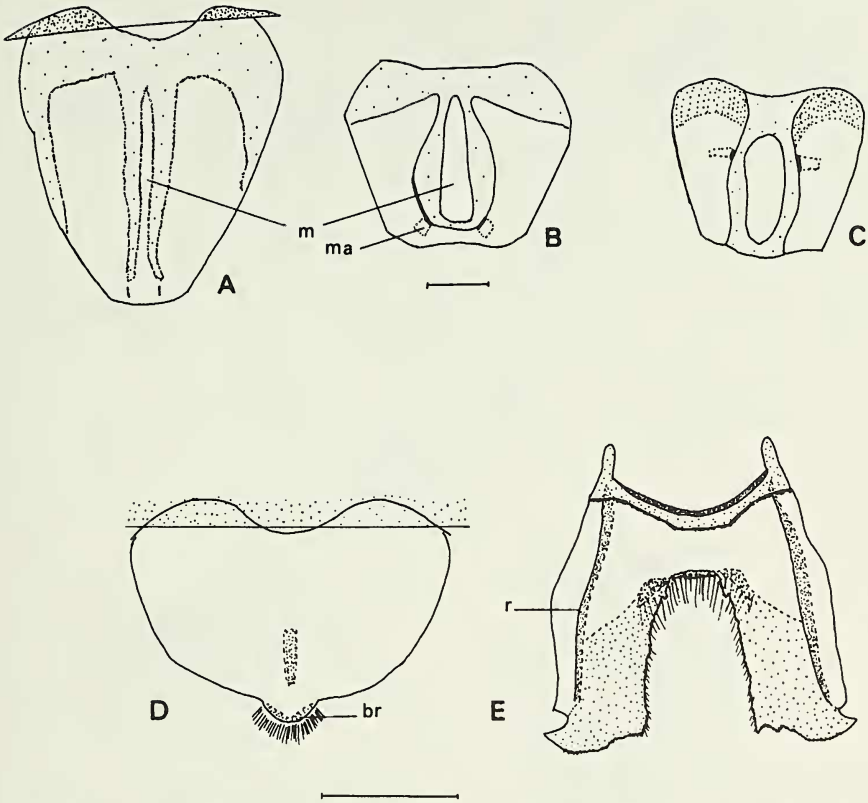

Figure 13 Male eighth terga and parallel ridge condition of sternum 8 (anterior at top). A. Tergum 8 (*Ankale maonica*); B. Tergum 8 (*A. viridis*); C. Tergum 8 (*A. grammodes*); D. Tergum 8 (*Dasylophia* sp.); E. Sternum 8 (*Dasylophia* sp.). br = brush, m = midplate, ma = muscle attachment, r = internal ridge. (Scale = 1.0 mm)

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with development of a long intrapleural membrane between the eighth segment and genital capsule (Miller, 1991).

Modifications of sternum 8 are often species- specific in Notodontidae (e.g., Franclemont, 1946; Forbes, 1948; Miller, 1987; Weller, 1990, 1992). Shape of the antecosta varies between and occasionally within monophyletic genera. In addition, hair-like androconia may be associated with membranous areas caudal to the antecosta. Such structures are found in some Phalerinae and Heterocampinae (Forbes, 1948). As in the tergum, lateral ridges and caudal structures of sternum 8 appear to provide sites for muscle attachment (Fig. 13E). Sternum 8 can bear a diversity of species-specific structures on the caudal edge. These range from a simple, glandular surface with hair-like scales (*Lepasta*, Fig. 14) to complex cuticular evaginations (*Marthula*, Fig. 15).

Female. Abdominal segments are rarely modified. Sternum 7 may have a patch of scent scales overlaying setae (e.g., *Dasylophia maxtla*

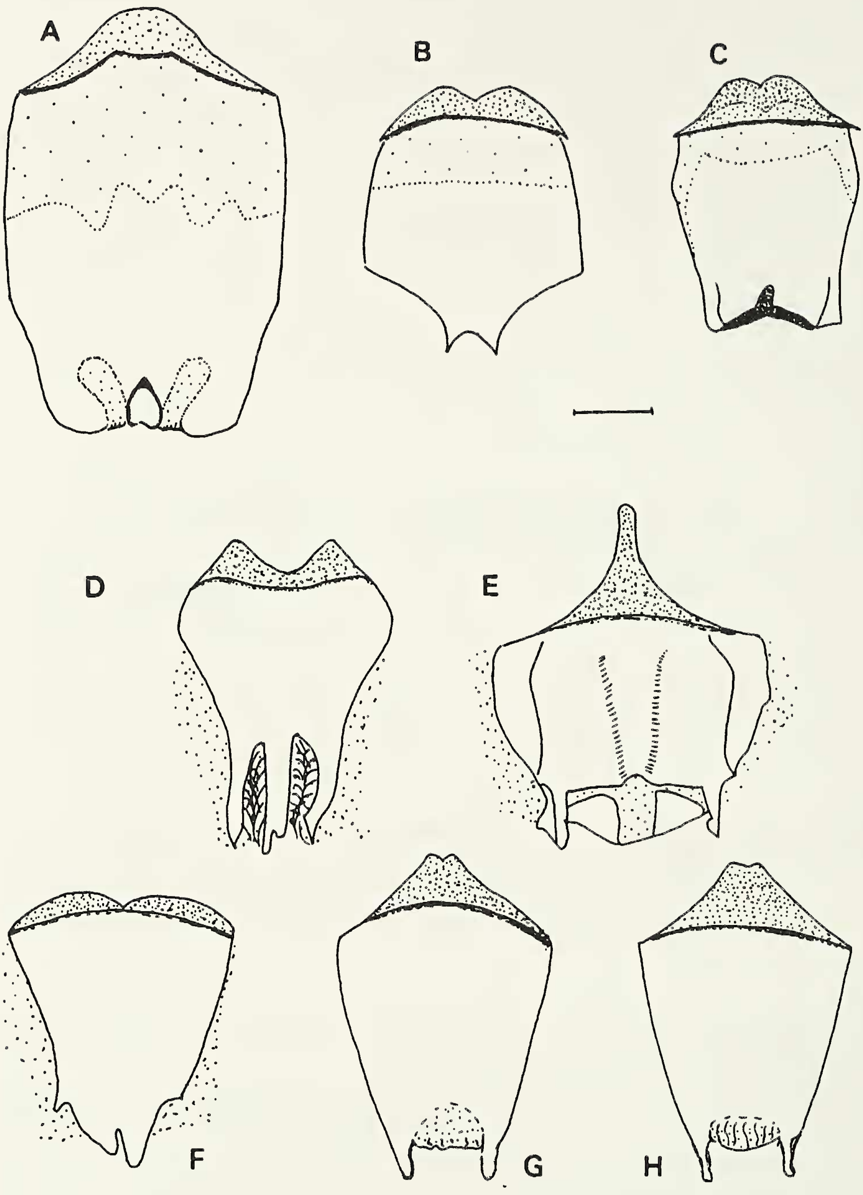

Figure 14 Male sternum 8 (anterior at top). A. *Ankale manacoides*; B. *A. viridis*; C. *A. maltha*; D. *A. maonica*; E. *Lepasta bractea*; F. *Antiopha* nr. *albosigma*; G. *Antiopha albosigma*; H. *Antiopha multilinea*. (Scale = 1.0 mm)

[Schaus]). In thaumetopoeines, sternum and tergum 7 form a continuous, lightly sclerotized ring that is covered with stiff deciduous hairs and scales. These scales may be a contrasting color (black or gold), and this "boule de laine" has been cited as a synapomorphy for the group (Kiriakoff,

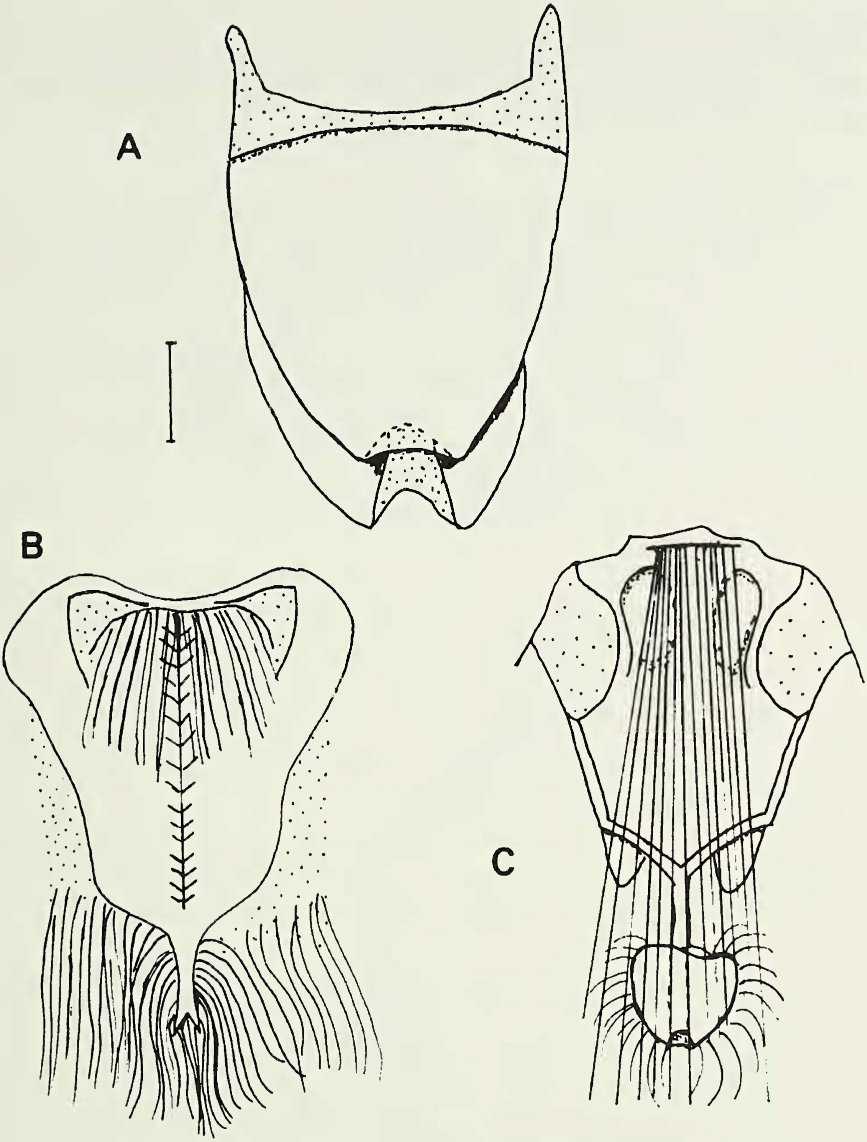

Figure 15 Male sternum 8 (anterior at top). A. *Marthula grisescens*; B. *Marthula mumetes*; C. *Marthula pulchra*. (Scale = 1.0 mm)

1969). However, the same modification also occurs in females of *Lobeza* Herrich-Schäffer, a large, neotropical species (male wingspan 63 mm, female 91 mm). Male genitalia and the larva (BMNH) of *L. Smithi* Druce are characteristic of Heterocampinae, suggesting that the continuous seventh tergal-sternal ring has evolved independently in *Lobeza* and thaumetopoeines.

Genitalia (Figs. 16-22)

Morphology of notodontid genitalia has been described (Forbes, 1948; Barth, 1955; Holloway, 1983; Miller, 1987, 1988, 1991 and references therein; Weller, 1990, 1991).

GENITALIA: MALE

Tegumen and vinculum (Figs. 16, 17). In Nystaleinae, the two halves of the vinculum are partially fused, and a sclerotized, caudal extension covers the base of the sacculus (Fig. 16). In most notodontids, the vinculum is rounded and the halves not fused.

When the tegumen and vinculum are fused, two nonhomologous conditions are found. In many neotropical notodontids, the tegumen-vinculum connection is fused in an S-shaped configuration (Fig. 16B). The other condition is typified by the holarctic genus *Pheosia* (Notodontinae). Here, the tegumen and vinculum form a single, fused C-shaped structure (Fig. 16D) presumably to support massive valves that articulate with it.

The uncus-tegumen juncture varies extensively (Fig. 17). The uncus and tegumen are sometimes completely fused, and have reinforcing, internal apodemes extending from the uncus into the tegumen (Fig. 17C,D). Apodeme shape and degree of fusion also varies. Apodemes may be absent, in which case the uncus base connects to the tegumen by a hinge of pleural membrane (e.g., *Calledema rufescens* Schaus). Usually, the tegumen-uncus connection is characteristic for a genus, but within *Calledema*, several configurations exist.

Uncus shape may or may not be characteristic for a genus. In some nystaleine genera, the distal process becomes membranous and setose (e.g., *Elymiotis*, *Poresta*). In some *Nystalea*, the distal process is curved and thin with an enlarged tip (Figs. 16A-C).

Above the anal tube and tegumen-uncus suture, paired, setose structures articulate on the venter of the uncus in Nystaleinae and many other notodontids (Figs. 16, 17). Kiriakoff called these structures gnathi (e.g., Kiriakoff, 1981), but Kiriakoff's use of the term is inconsistent with both Pierce (1914) and common usage. Pierce described the gnathos as a "free ring, enclosing the anus," and reserved the term socii for hairy pads arising from the base of the uncus. Forbes (1923) applied the term gnathos to part of the subscaphium located below the anal tube. Klots (1970), following Pierce, suggested that the gnathos is derived from the caudal edge of the uncus and glabrous, whereas socii were derived from the uncus base and setose. In several notodontid species, these setose structures are fused to the base of the uncus (e.g., Phalerinae). The term socii appears to be most appropriate for these structures.

Valve (Figures 16, 18, 19). The valve in many species of neotropical notodontids (e.g., some Heterocampinae, most Nystaleini (sensu Miller, 1991), *Pentobesa*, many Dioptinae and Hemiceratini) have a membranous, highly pleated sacculus (= corrugated sacculus; Holloway, 1983)

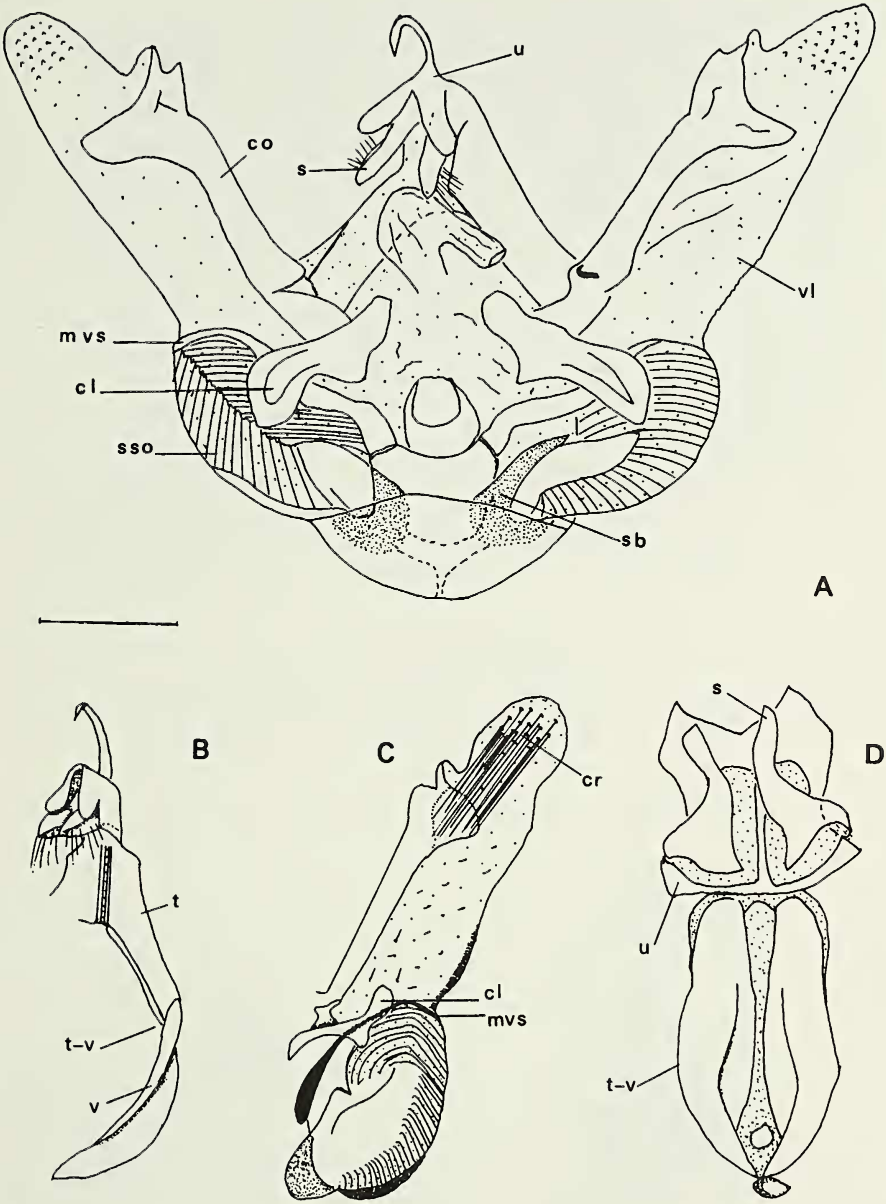

Figure 16 Male genitalia. A. *Nystalea aequipars*; B. caudal view of tegumen, vinculum and sociuncus of *Nystalea virgula*, valve removed; C. right valve of *Nystalea virgula*; D. *Pheosia tremula*, valvae removed. cl = costula, co = costa, cr = coronalike structure, mvs = midvalve sclerotization, sb = sclerotized base of sacculus, s = socius, sso = saccular scent organ, t = tegumen, t-v = tegumen-vinculum junction, u = uncus, v = vinculum, vl = valvula. (Scale = 1.0 mm)

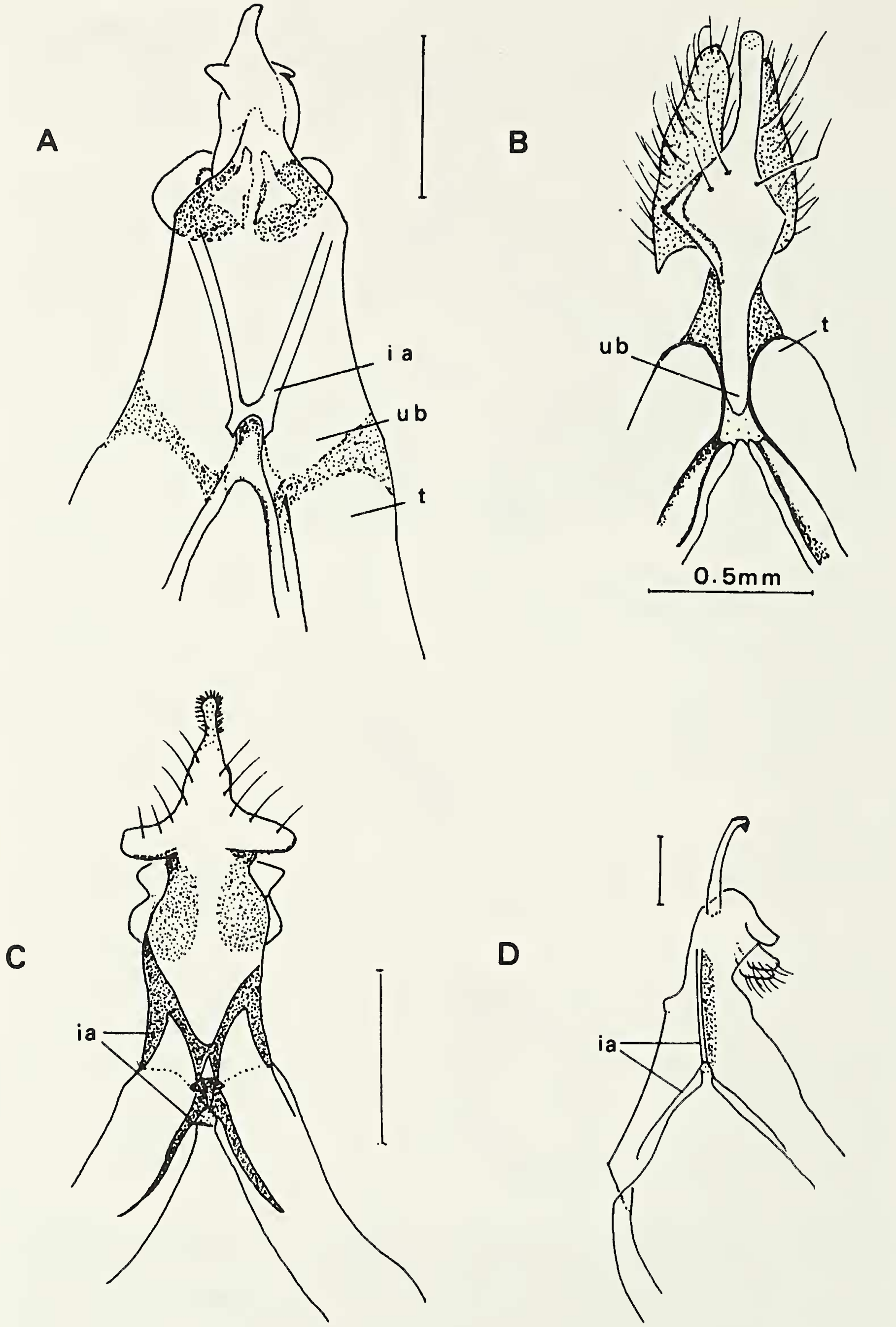

Figure 17 Dorsal view of uncus-tegumen attachment. A. *Elymiotis ancora*; B. *Gopha mixtipennis*; C. *Poresta joanna*; D. *Nystalea aequipars*. ia = internal apodemes, t = tegumen, ub = uncus base. (Scale = 1.0 mm)

(Fig. 16). A mix of long hair-like and spatulate scales arises from its base. Barth (1955) demonstrated that a gland is located within the sacculus of *Hemiceras proximata* Dognin, and suggested that it produces pheromones. I refer to the pleated sacculus with associated hairs as the **saccular scent organ** (SSO) (Weller, 1989, 1990). Although pheromone producing organs and androconia are often associated with male genitalia (e.g., coremata of Arctiidae), this is an unusual example of the primary genitalic structures being themselves pheromone-producing. Typically, a sclerotized band separates the SSO from the rest of the valve. This midvalve sclerotization (Weller, 1990) appears to divide the valve into costal and saccular compartments. This sclerotization can be expanded as in *Pentobesa* or *Bardaxima*. Occasionally, the midvalve sclerotization is reduced and the SSO is not distinct from the remainder of the valve (e.g., *Lysana plexa*: Nystaleinae; *Disphragis tharis*, *Rifargia lineata*: Heterocampinae). In these, the flattened SSO does not expand as greatly. In some species, a modified saccular base occurs in the presence of an SSO. Here, a small hook or ridge is present that presumably provides an anchor for the valval flexor muscles (M5: Forbes, 1939b; Tikhomirov, 1979).

The SSO is variously developed within and between genera. It can be greatly enlarged as in *Marthula* and many Dioptinae. In some species of the Hemiceratini (e.g., *Hapigia*, most *Hemiceras*), the sacculus is greatly elaborated and enfolds a large scent pencil (Fig. 18). I refer to this

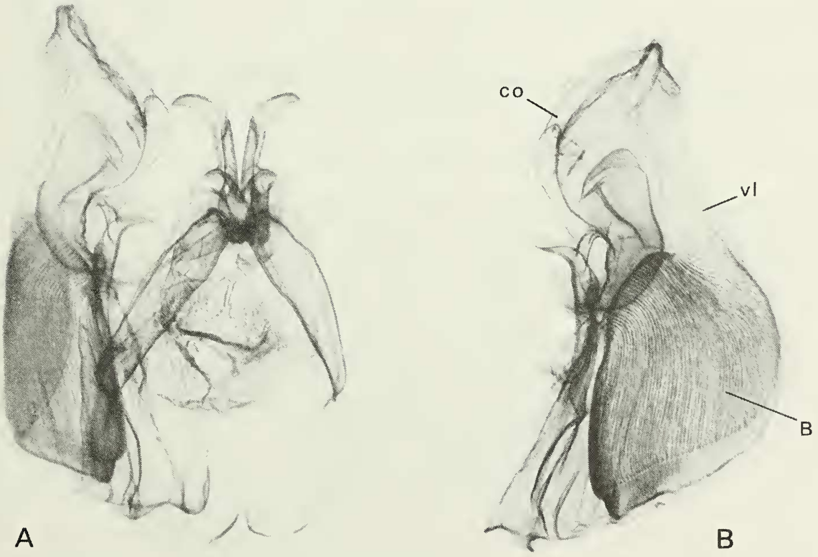

Figure 18 Male genitalia of *Hemiceras constellata* showing the Barth valve. A. Genitalia with right valve removed; B. Right valve. B = Barth valve (= sacculus), co = costa, vl = valvula.

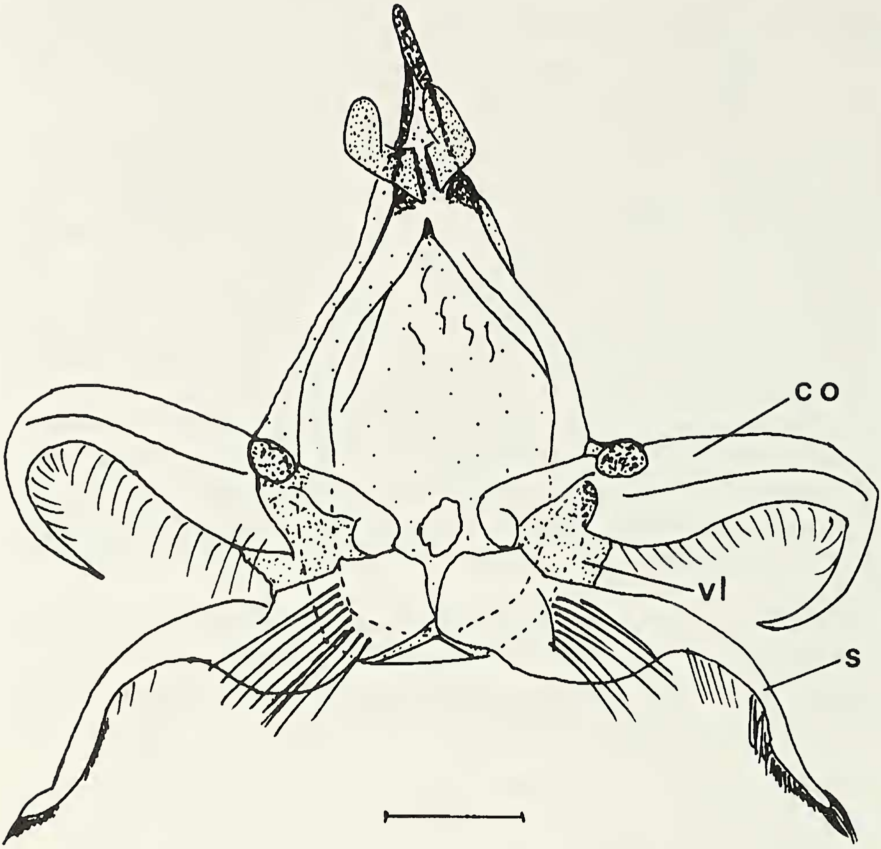

Figure 19 Male genitalia of *Dasylophia colimata*. co = costa, s = sacculus, vl = valvula. (Scale = 1.0 mm)

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complicated SSO as the Barth valve, in honor of Dr. R. Barth and his pioneering studies on the Brazilian fauna.

The SSO can also be reduced in a variety of non-homologous conditions. In *Pentobesa* and some members of the *Dasylophia*-group, the SSO is usually moderately developed, the pleats are less numerous than in nystaleines, and the sacculus is smaller. Pleats are completely absent in some representatives of the *Dasylophia*-group, and the sacculus is sclerotized (e.g., *D. colimata* Dyar, Fig. 19).

In many notodontids, the costa is a massive structure with various projections along its length. These are uncommon in Nystaleinae. The costa of nystaleines is usually a thin, sclerotized rod that may or may not extend completely to the apex of the valve. In *Nystalea*, the dorsal edge is sclerotized for two-thirds the length of the valve and widens into a characteristic shape (Figs. 16A, 16C). Beyond this widening, the distal portion is membranous with short setae and stiff hairs analagous to a noctuid corona (Forbes, 1954).

In nystaleines, some hemiceratines, and some heterocampines, a sclerotized process arises proximally from the dorsal edge of the costa, and extends into the anellus. Muscle attachments occur at its base (Fig. 16). Presumably, these structures, in conjunction with the socii, uncus and costa, provide traction in copula. Forbes (1948) suggested that these processes might be homologous with structures in the geometrid genera *Himera* Duponchel and *Nacophora* Hulst, and with the hairy pads of Thyatiridae. From limited observations, I conclude that the processes in these three families are not homologous. I refer to this structure as the **costula** (Latin: little rib) (Weller, 1990), distinguishing it from the costal process of the sacculus (Forbes, 1954). The costula appears to be a modification of the noctuoid transtilla, and its shape is usually species-specific. Dioptines lack costulae, and instead have a fused transtilla that arises from the base of the costa (Miller, 1991).

A membranous region occurs between the sclerotized costa and midvalve sclerotization in nystaleines. This region varies from being slightly to extremely pleated (*Bardaxima*), and has scattered setae or patches of setae and hairs (Figs. 16A, 18). It appears to be homologous with the valvula of Pierce (1914) (Weller, 1990).

Anellar Region. The anal tube is often weakly sclerotized ventrally in thin vertical strips. Ventral to the costulae, scattered setae occur. The juxta is sclerotized and varies from slightly to extremely concave in nystaleines. In other notodontids, the dorsal edge of the juxta may be elaborated into an aedeagus guide or stabilizer (e.g., *Lirimiris*).

Aedeagus (Fig. 20). In Nystaleinae, the vesica (= endophallus; Klots, 1970) tends to be bulbous, terminating in a narrow tube that is directed cephalad. Deciduous cornuti, present in many genera, vary in size and shape (Forbes, 1948; Holloway, 1983).

Many modifications of the aedeagus occur (Fig. 20A-E). The distiphallus may have long processes (*Symmerista*) or small flanges (*Notela*). The basiphallus can be shovel-shaped (Fig. 20E) or tubular (Fig. 20C). Often, a ventral sclerotized piece occurs on the basiphallus that may provide extra surface area for muscle attachment. I call this an **aluta** (Latin: shoe of soft leather). This structure, which is attached to the manica, can be flat and sheetlike, caecum like, or bowl-shaped (Fig. 20D).

The aluta of *Nystalea* and related genera is an enlarged, tubular structure that has a characteristic triangular exit for the ductus seminalis (Fig. 20A, B). Large muscles attach both dorsally and ventrally (Weller, 1989, 1990; Miller, 1991). The term **callosum** (Latin: hard skin; Weller, 1990) has been used to refer to this specialized aluta, and it only occurs in Nystaleinae (Weller, 1989; Miller, 1991).

GENITALIA: FEMALE (FIGS. 21, 22)

Notodontid female genitalia show greater morphological variation than is usually found in the Noctuoidea, and it is not uncommon for them to be species-specific (Weller, 1992). However, within species complexes,

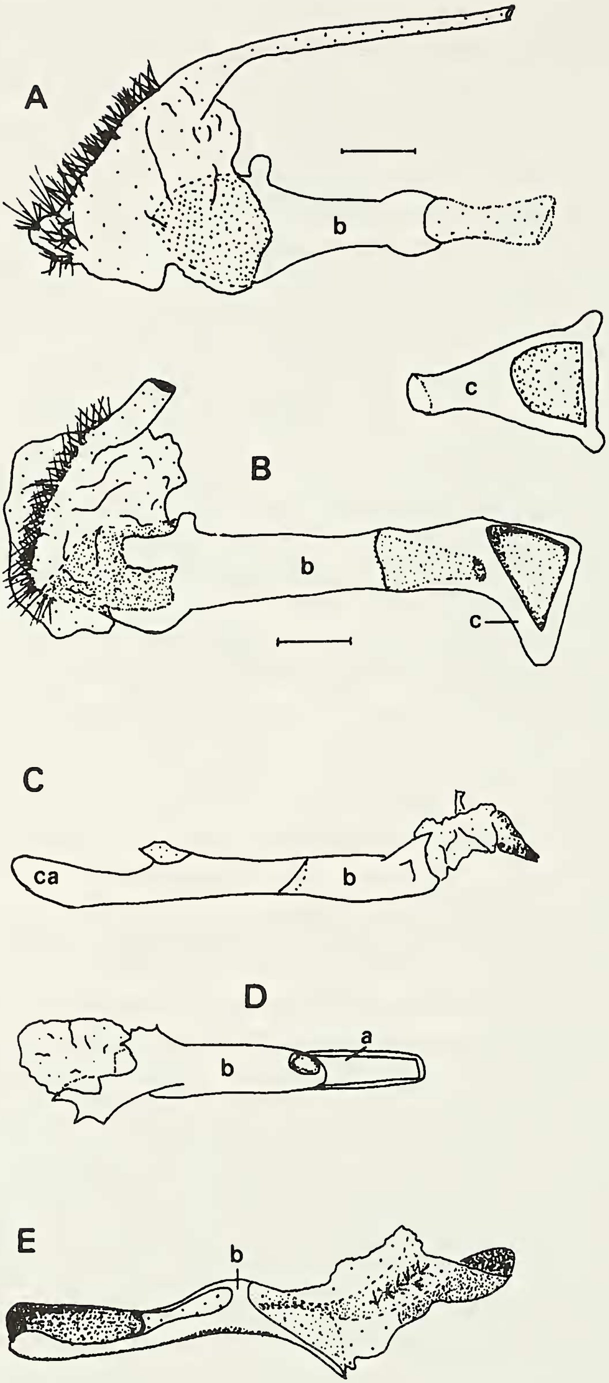

Figure 20 Aedeagii. A. aedeagus with callosum removed (*Nystalea similis*); B. callosum (*Nystalea aequipars*); C. caecum (*Hemiceras* sp.); D. caecum with aluta (*Nadata gibbosa*); E. plain tube with aluta (*Rifargia lineata*). a = aluta, b = basiphallus, ca = caecum, c = callosum. (Scale = 1.0 mm)

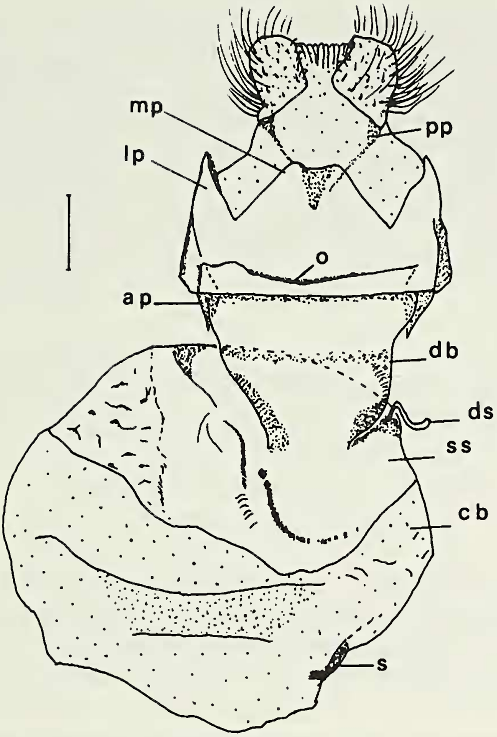

Figure 21 Female genitalia of *Nystalea aequipars* (ventral view). ap = anterior apophysis, cb = corpus bursae, db = ductus bursae, ds = ductus seminalis, lp = lateral prominences on eighth sternum, mp = midventral prominence, o = ostium bursae, pp = posterior apophysis, s = signum, ss = sclerotized shield. (Scale = 1.0 mm)

female structures (e.g., lamellae antevaginalis, tergum 8) tend to have similar shapes (e.g., *N. aequipars* species complex; Weller, 1990).

Ovipositor Lobes. The papillae anales are usually membranous, but may be lightly or heavily sclerotized. In Nystaleinae, they are usually covered with short, scattered setae with longer, inwardly curved setae arising from the base. The lobes may be flattened and covered with stout, curved setae (e.g., *Notoplusia*, *Lyricinus xylophasioides*). In *Apela* Walker (Hemiceratini), the ovipositor setae resemble shepherd crooks. Ovipositor lobes of the neotropical heterocampine *Rhuda dimidiata* are concave, and the setae are long and curved with wide, spatulate tips. Other species of *Rhuda* have unmodified setae.

In nystaleines, posterior apophyses are typically long and slender, although they can be short and stout (e.g., *Calledema rufescens*). In *C. rufescens*, a sclerotized invagination is located dorsally between the papillae anales and tergum 8 (T8). Presumably, this invagination is associated with a pheromone gland.

Sclerites of the Eighth Abdominal Segment. The shape of T8 and

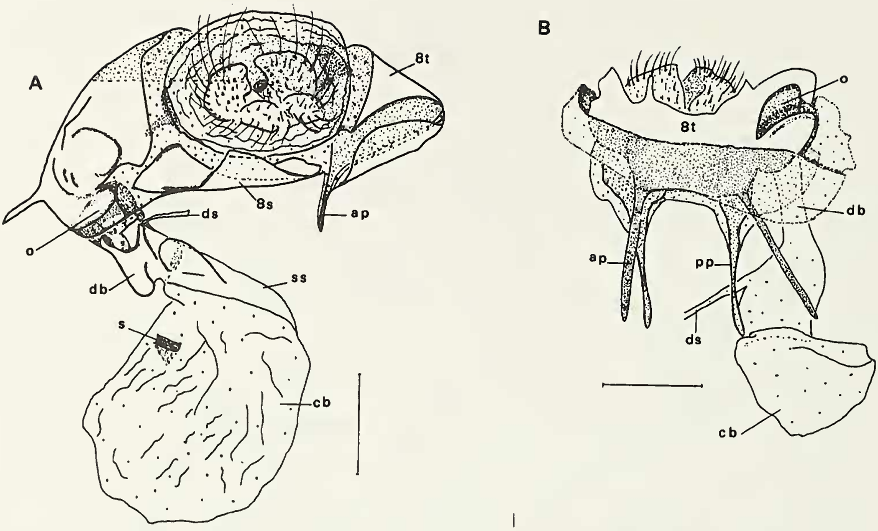

Figure 22 Asymmetrical female genitalia. A. ventral view, *Dasylophia maxtla*; B. dorsal view, *Pentobesa poecila*. ap = anterior apophysis, cb = corpus bursae, db = ductus bursae, ds = ductus seminalis, o = ostium bursae, s = signum, ss = sclerotized shield, 8t = eighth tergum, 8s = eighth sternum. (Scale = 1.0 mm)

S8 varies within and between nystaleine genera. Some species possess lateral processes on only the sternum or on both sternum and tergum. Some have additional lateral processes on the lamellae antevaginalis. The ostium bursae is usually very wide, extending nearly the entire width of S8 (Fig. 21). Some females have asymmetrical genitalia, and in these, the ostium bursae is usually located left of center. Asymmetrical genitalia are common in *Pentobesa* and the *Dasylophia terrena*-species group. In *Pentobesa poecila* (Felder), the ostium bursae is dorsal, located on the enlarged, distal edge of the apophysis (Fig. 22A). In *Dasylophia maxtla* (Schaus), the left anterior apophysis is reduced, and the ostium is located slightly ventral to the apophysis (Fig. 22B). The male genitalia in these species are also asymmetrical. Asymmetrical female insect genitalia are rare (reviewed in Eberhard, 1985). The ostium bursae of many notodontid females have various structures covering or blocking it (e.g., *D. anguina* [Smith], *Gopha mixtipennis*, *Heorta roseoalba*: Heterocampinae).

Other Structures. The ductus bursae may be membranous, partially or completely sclerotized. In nystaleines, it is often sclerotized and dorsoventrally flattened (Fig. 21). In this case, the lateral margins are membranous, allowing them to expand into a rounded tube. The ductus bursae may be extremely short (e.g., *D. anguina*) or extremely long (e.g., *Hapigia* spp.: Hemiceratini), two to three times the length of the corpus bursae.

In Nystaleinae, the ductus seminalis often arises from the left ventral area of the corpus bursae (Fig. 21). However, it may also arise from near the ostium bursae, from the ductus bursae (Fig. 22) or from other areas of the corpus bursae. The corpus bursae itself may or may not be partially sclerotized. Where ductus and corpus bursae meet, there may be internal spinules or other modifications as in *Pentobesa lignicolor* Möschler or *Marthula mumetes* where a "necklace" of spines surrounds the mouth of the corpus bursae. Single or multiple signa are present, and their shape may be species-specific.

Summary of Morphological Trends

Although the morphology of Nystaleinae and other notodontids is difficult to characterize, certain trends can be noted. Mouthpart structures tend to be well developed in neotropical species and reduced in nearctic species. As in many Lepidoptera, female antennae are usually simpler than male. The prothorax usually has parapatagia; occasionally an additional lateral pair occurs. The tympanum may have all four pockets, with the fourth characteristically being "open," that is, with anterior and posterior struts not connected by a sclerotized sheet. Loss or reduction of pocket II is frequent in notodontids, and pocket III has been lost in all dioptines examined. Further tympanal reduction occurs in some dioptines and thaumetopoeines.

Species can often be assigned to genera based on female genitalic structures, but the diversity of both female and male genitalia makes generalizations difficult. When other tribes and subfamilies are more thoroughly surveyed, statements on genitalic trends in the family may be possible.

Several types of previously undescribed sexually dimorphic structures occur on male legs, wings, abdomen and genitalia in neotropical notodontids. Some species have androconia and glandular areas on both legs and genitalia (many nystaleines), on both pre-genital abdominal segments and genitalia (*Marthula*, *Hapigia*), or on all three areas (*Calledema*). The cteniophore is the only structure previously surveyed that has been ascribed a possible courtship function (McColl, 1969). A survey of these structures with more rigorous characterization of their function should be undertaken in light of these findings.

Summary of Morphological Terms and Synonyms

Aluta (new term)(Fig. 19D): sclerotized piece of cuticle attached to the ventral surface of the basiphallus. May have originated as an extension of the manica. Found in most notodontids.

Anterior branch pocket (new term)(Fig. 5): small pocket ventral to the tympanic cavity formed from an extension of the anterior branch of pocket IV. Found in some *Hemiceras* and some nystaleines.

Barth valve (new term)(Fig. 17): valve with sacculus enfolding a hair pencil that emanates from the saccular base. Associated gland occurs within sacculus. Found in *Hapigia* and most *Hemiceras*.

Callosum (Weller, 1990)(Fig. 19A, B): specialized aluta enclosing the basiphallus, usually with a footlike projection. Unique to Nystaleinae.

Costula (Weller, 1990)(Fig. 15): sclerotized process arising from the base of the male valval costa. Occurs in nystaleines, some heterocampines and hemiceratines, and appears to be a modification of the noctuoid transtilla.

Epimeral pocket (new term)(Fig. 5): small pocket located on the pre-epimeron/epimeron suture of the metathorax. Found in some nystaleines, hemiceratines and heterocampines.

Epimeral ridge (new term)(Fig. 5) (= "le support anterior" of Kiriakoff, 1950a, 1950b, 1950c): an internal ridge located at the pre-epimeron/epimeron suture of the metathorax that extends anteriorly from the tympanic cavity. Found in some nystaleines, hemiceratines and heterocampines.

Midplate (Weller, 1990)(Fig. 13): sclerotized area, sometimes with ridges, located in the middle of the male eighth tergum. Occurs in many notodontids.

Midvalve sclerotization (Weller, 1990)(Fig. 15): ribbonlike or expanded plate of sclerotized cuticle located on the inner mesal surface of the male valve, demarcating the dorsal edge of the sacculus. Occurs in many nystaleines, hemiceratines and dioptines. Usually associated with a pleated sacculus.

Peniculus (Fig. 12B, 13)(Thiaucourt, 1985): similar to a cteniophore, but pleural expansion is reduced. It occurs on male abdominal sternum V in *Calledema rufescens*.

Pleural hood (Fullard, 1984): expanded pleural membrane that surrounds the first abdominal spiracle, and cups the tympanal opening. Analogous to the noctuid tympanal hood. Occurs in *Hapigia* and *Antaea*.

Pocket IV (Richards, 1932)(Figs. 5, 6) (= "le support posterior" of Kiriakoff, 1950a, 1950b, 1950c): tympanal pocket located ventral to the tympanal cavity that is usually "open" with an anterior and posterior ridge defining its location. Anterior ridge reduced or absent in some notodontids (Kiriakoff, 1950a,c). Pocket IV has its opening towards the tympanal cavity when a sclerotized sheet connects the anterior and posterior supports (= "closed" condition). This pocket occurs in many notodontids.

Saccular scent organ (Weller, 1990)(Fig. 15): membranous and pleated sacculus with scent scales emanating from the base. Found in numerous neotropical (Weller, 1989) and asian species (Holloway, 1983).

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